THE STRUCTURE AND RELATIONSHIPS OF CERTAIN ELEUTHEROZOIC PELMATOZOA.

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INTRODUCTION.

As a result of observations covering several years both in the laboratory and in the field, it has become increasingly evident that many of the commonly accepted ideas relative to the habits of the Pelmatozoa are in need of a considerable amount of revision. I have been fortunate in having the extensive collections of Mr. Frank Springer and of the United States National Museum placed at my disposal for study, and the observations made upon this material and embodied in the present paper go far toward establishing the conclusions here set forth. I wish here to express my thanks to Mr. Springer and to Dr. R. S. Bassler for the many favors extended to me during the preparation of this paper, and I am further indebted to Dr. Bassler for help received in the preparation of a number of the illustrations here used. Mr. Austin Hobart Clark, of the United States National Museum, has reviewed my manuscript and has very kindly offered a number of valuable suggestions. Advantage has been taken of these in several instances, and in all cases are accredited to him where used.

The division of the Echinoderma into two grades, Pelmatozoa and Eleutherozoa, clearly reflects the common concept of the Echinoderms as consisting of freely moving forms on the one hand and statozoic types on the other. As a matter of fact no sharp line of demarcation may be drawn on the basis of the relative freedom of the animals, for the Pelmatozoa, or supposedly statozoic echinoderms, show this character to but an indifferent degree. It is probable indeed that we may hold the Edrioasteroidea alone as consistently affixed types.

SYSTEMATIC DISCUSSION.

In the following paper an attempt is made to bring together some of the more important points relating to certain Pelmatozoa that for a part of their lives lead a free or semifree existence. Other forms

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that have no jointed column, but nevertheless are attached, usually by a short thick stalk, are likewise discussed. These Pelmatozoa in a way are to be regarded as intermediate between the statozoic and eleutherozoic forms, as regards their mode of life, and may be dealt with to advantage in the present paper. Material throwing not a little light on certain questions concerning these various types has become available and the evidence thus afforded may prove of some interest.

There are many well-known eleutherozoic Pelmatozoa, but it seems probable that the assumption of a free or semifree existence has been far more prevalent among these forms than is generally conceded. Aside from the mere enumeration of the eleutherozoic forms, a discussion of the structure of the animals is given in so far as this may throw light on their genetic affinities. In some cases where the observed facts seem to warrant the drawing of conclusions in regard to the derivation and relationships of a certain type, this has been done. The assumption of an eleutherozoic existence by certain Pelmatozoa is of interest as bearing not only on the forms affected, but also on the habits of the Pelmatozoa in general. For this reason the influence of an eleutherozoic existence on the distribution and segregation of the Pelmatozoa has been indicated though not treated in any considerable detail. Finally, a general though brief discussion of the maintenance of such a life among the Pelmatozoa in its various aspects is given.

It is here held the Echinodermata as we now know them are descended primitively from an eleutherozoic stock. The eleutherozoic archetype gave rise to a line of descendants among which a sessile habit was gradually assumed. This form of life became deeply ingrained in the fiber of the stock, and has left an indelible impress on the structure of the organisms. When the term "eleutherozoic stock" is hereafter used the primitive organisms that had not as yet acquired a sessile habit are meant. Similarly by "statozoic or sessile stock" we designate that body of echinoderms among which a fixed mode of life was primarily assumed. It may well be that absolute fixation did not obtain in all the phyletic lines of the Echinodermata. In the case of the Holothurioidea particularly the evidence is highly inconclusive.

A tendency to break away from the sessile echinoderm stock and to reassume a free mode of life is to be observed from practically the earliest times to the present. Springing from the early, less specialized statozoic echinoderms, certain of these aberrant forms established lines that have been perpetuated as the great classes of the Eleutherozoa. It is not within the scope of the present paper to deal with these large groups except in a very general way. In later times, as offshoots from the more highly specialized Pelmatozoa, the

eleutherozoic types appeared sporadically, founding, as a rule, short-lived lines that although successful in a small way, had the Pelmatozoan structure too deeply impressed upon them to permit of any considerable deviation from the parent stock.

With the possible exception of the Holothurioidea, we may hold, I think, that such eleutherozoic echinoderms as are known to us have been derived from statozoic ancestors. It is but natural that upon the acquisition of a detached or semidetached form of life changes should begin to appear in the structure of the organism. If given sufficient time, these changes so deeply affect the structure of the animal that it is a very difficult matter accurately to establish lines of descent. This is true to a far greater extent than among those forms that remain attached. Among the latter evolution of adult characters is largely orthogenetic in its tendencies, and it is possible to reconstruct the ancestral forms as well as predict the types to come with a fair degree of certainty. In the case of the eleutherozoic forms, however, we have one newly acquired set of tendencies superimposed upon another set. These secondary tendencies, induced as they are by a form of life widely at varience with that under which the first set operated, tend to vitiate the force of many of the primary tendencies, if not indeed to nullify some of them. In addition certain of these newly acquired tendencies initiate structural changes which diverge widely in their nature from the given line of evolution, and are of such a type as largely to mask and render unintelligible the characters that go to help in determining the genetic affinities of the animal. Such being the case, one's efforts to establish relationships among these aberrant forms are apt to be unsatisfactory at best. In many cases, however, the eleutherozoic Pelmatozoa stand so near the points of inception of their several lines that the problem is not greatly complicated by the presence of altered or superimposed structures.

DIVISIONS OF THE PELMATOZOA.

The Pelmatozoa to be discussed may be divided into three main groups:

I. Those forms retaining jointed columns throughout life, but not using them for permanent attachment.

II. Those forms which at some stage of development permanently lose all or the greater part of their columns, becoming truly eleutherozoic.

III. Those forms that are permanently attached by means of a base of varying composition as regards the constituent elements. No true jointed column is present. The members of this group I shall here style pedunculate forms, for convenience of reference.

This grouping, as well as other classifications employed throughout the paper, is a purely artificial and arbitrary one. The intention is merely to bring such forms together as show a certain similarity in structure, and thus aid in simplifying the discussion of the modifications exhibited by different types.

As might be expected, one genus may contain species that fall under two different groups, as, for instance, *Edriocrinus*, certain species of which belong to Group II and others to Group III. Even a single species may have representatives referable to two different groups. Thus certain specimens of *Millericrinus prattii* may be referred to Group I, while by definition other individuals fall in Group II.

Group I.

The group comprising those forms that do not become detached from their columns, and yet, during a portion of their lives at least, are capable of more or less free movement, is a very large one. As a matter of fact, it is probable that the greater part of the Pelmatozoa, with the exception of the Edrioasteroidea and those forms here included in Group II, are safely referable to this assemblage. This is a sweeping statement, but one thoroughly justified, I believe, by the evidence at hand. In referring to an eleutherozoic period during the lives of the Pelmatozoa, one is meant subsequent to the free-swimming larval stage, and after the formation of a column. In most cases, perhaps, this period of detachment from the bottom came at a comparatively early stage in the ontogeny of the animals, and was followed by the reattachment of the organisms. Frequently, however, the animals retained their freedom throughout life. Again, it is probable that in the lifetime of some forms at least there were several alternating periods of attachment and freedom. In the case of some of the Cystidea, it is possible that the animals were never firmly affixed at any stage in their development. In the discussion of this group the Cystidea will be dealt with first, to be followed in turn by the Blastoidea and Crinoidea.

CYSTIDEA OF GROUP I.

It is probable that a large proportion of the Cystidea led a free or semifree form of existence. Many were undoubtedly capable of active movement, while others, attached or unattached at will, were comparatively passive. It is but natural that eleutherozoic forms should be more abundant among the Cystidea than among the Crinoidea or Blastoidea, for they more nearly approximate to the eleutherozoic archetype of all the Echinoderma. With the Cystidea, then, in some cases, the eleutherozoic forms may be considered in the light of organisms which had not yet attained true pelmatozoan fixation. In other lines fixation, though acquired, was such a novel

character and became so irregularly effective that the return to a purely eleutherozoic habit was a comparatively simple matter. In the case of the Blastoidea and Crinoidea, however, the free forms represent aberrant types which have reverted to this type of existence after a considerable period of perfected fixation.

Divisions of the Cystidea of Group I.—The eleutherozoic Cystidea may be divided into three "types" or subgroups for the purpose of convenience:

1. This type is reserved for certain Cystidea which did not have true columns, but when attached at all, were cemented to the bottom by an outgrowth from the body wall. It seems possible from the evidence at hand that certain of these forms were free-swimming or floating organisms, at least during a portion of their lives.

2. In this type are placed those Cystidea provided with a prehensile column which attached themselves at will, probably not by cementation, but rather by looping the distal portion of the stem about some fixed object.

There is a group of Crinoidea directly comparable with these forms.

3. This type includes those Cystidea which propelled themselves along the bottom, making use of their brachioles and possibly their columns as organs of locomotion.

CYSTIDEA, TYPE 1.

In this group are chiefly to be found those primitive, many-plated Cystidea which had not yet evolved a column for purposes of attachment. These are the forms that in this regard represent the connecting link between the eleutherozoic echinoderm ancestor and the Pelmatozoa. With them fixation was a novelty, and in many of the more primitive types, no doubt, was irregularly acquired in the different lines. In some cases a very rudimentary stem seems to have been present, but the possession of such an organ appears to have been an indifferent character at best. The stem apparently might be absent or not, within the limits of a single species, and when present probably functioned in the same way as the stem in those genera referred to Group III.

The genera referred by Bather to the families Aristocystidæ and Echinosphæridæ may all provisionally be placed in this group. Permanent attachment by cementation to the bottom undoubtedly occurred in many forms, at least in the adult stages, and as noted above, rudimentary stems are occasionally present. In many cases, however, it seems probable that the period of fixation, if there were such, was of but short duration and irregular occurrence.

Echinosphæra.—The genus *Echinosphæra* may be taken as characteristic of the group. The conclusions to be drawn from the evidence afforded by this genus may be held to apply with greater or less force to the other forms here referred. *Echinosphæra aurantium*, Plate 1,

figure 11, has a subglobose theca composed of a great number of irregular, polygonal plates. These plates are remarkably thin, and, considering the size of the animal, the skeletal structure must have been exceptionally light. In a Russian specimen of average size the plates measured but 0.25 mm. in thickness. Even this does not represent solid stereom, as the substance of the plates is traversed by innumerable series of radiating tubes. The brachial appendages were no doubt comparatively slender and weak.

In the aboral portion of the theca there is usually a slight projection, which when present doubtless served as a point of attachment for the organism. This protuberance is apparently an evagination of the body wall and seems to be restricted to no closely circumscribed area as to location, other than that it is near the aboral pole. So far as the descriptions of the species are concerned, this projection seems to be constantly present in European specimens. In the American forms, which are apparently specifically identical with the European, the protuberance is apparently wanting at times, but a cicatrix marks its former location. There are signs of resorption and secondary deposition of stereom, indicating that although attached at one time the animals had subsequently become free.

Even when present, this projection, because of its relatively insignificant size, seems quite inadequate as a support for an adult animal. So far as I have been able to see in the specimens I have examined the distal end of the projection shows no signs of attachment such as one would expect to find were the animals cemented to the bottom at the time of their death. Rather, the free end seems irregularly broken, but not exhibiting in many cases the clearly defined angles of a fresh fracture. Furthermore there is no considerable thickening of the plates of the pedicle as preserved and no obliteration of sutures, features that are usually characteristic of that portion of a Pelmatozoan lying in immediate proximity to the point of cementation.

Again, if the adult cystids were attached by means of such a short pillar, it seems probable that the area immediately surrounding the point of attachment would be more or less in contact with the bottom and would show signs of such apposition. This is especially to be looked for in cases where the point of attachment is asymmetrically located at some distance from the aboral pole as in Plate 1, figure 11. No signs of abrasion or contact modifications are to be noted, however.

In other many-plated Cystidea that were unquestionably affixed to the bottom in their adult stages evident signs of attachment are to be observed. An examination of the figures of *Aristocystis*, *Fungocystis*, and *Craterina* as given by Barrande clearly shows the effect of such cementation. In *Aristocystis bohemicus*, Plate 1, figures 1, 2, the animal is cemented to a gastropod shell which it has

almost completely grown over. It is to be noted that the area immediately surrounding the point of attachment is smooth and of quite different appearance than the remainder of the theca. Again in the case of figures 7, 8, which represents the base of another specimen of the same species, as well as in figures 9, 10, where the theca was turned at somewhat of an angle to the plane of the area of attachment, it may be seen that one side of the theca, which apparently grew in contact with some object, is quite smooth. In all these genera mentioned, the area of attachment is large and well defined.

It may be argued that *Echinosphæra* has a column of sufficient length to raise the theca above the bottom and thus preclude the possibility of contact phenomena and other features to be observed in the genera cited above. This argument is inadmissable, however, on various grounds. In the first place the sometimes extremely excentric location of the fragment retained would not permit of such support. Again the extremely small size of the pedicle compared to that of the theca makes such an hypothesis quite untenable.

Were a column to have been acquired by certain forms of *Echinosphæra* it could not have approached that possessed by *Arachnocystis* in degree of specialization. These columns, as figured by Barrande in the case of *Arachnocystis infaustus*, were never of any considerable length, and apparently were never attached permanently to the bottom.

I think that one is justified in concluding that fixation did not obtain in the adult stages of *Echinosphæra*, at least in the majority of individuals. It seems probable that at some comparatively young stage in the lives of the animals fixation by cementation took place. Subsequently the cystids became detached. Occasionally fixation may have persisted throughout life.

In connection with this apparent lack of consistent fixation in the case of *Echinosphæra* must be considered the enormous range of the genus. Originally described from the Baltic region, *Echinosphæra* has been found throughout the United States from the Appalachians to the Rocky Mountains. Notwithstanding its great horizontal range, its vertical range is very small, at least in the United States, where it is restricted to a well-defined zone. Moreover, as mentioned above, the American species is probably specifically identical with the Baltic. *Echinosphæra aurantium* then has quite as great a range as *Uintacrinus socialis*. Such wide distribution argues for a pelagic habit, but one hesitates to apply this explanation to *Echinosphæra*.

One may conceive perhaps that *Echinosphæra* might have been a floating organism. The extremely thin plates and consequent lightness of the animal might well indicate adaptation to such a form of life. The globose theca likewise points in the same direction. The specific gravity of certain Echinoderms is at no time so very much

greater than that of the surrounding medium. A decrease in the weight of the animal, by a reduction of the amount of calcareous matter to the minimum, and perhaps an increase in the buoyancy of the organism, by an inconsiderable accumulation of gas within the body would serve to reverse conditions. Movement of the brachial appendages, however slight, would aid in sustaining the animal.

If *Echinosphæra* were indeed a floating organism, it could have been transported these great distances by current action. Certainly one would not expect the comparatively weak brachioles to perform very great service as organs of locomotion. Nor could the transportation of the larvæ alone account for the wide dispersal of the species. If we attribute such powers of dispersal to the larvæ of *Echinosphæra*, how may we well deny them to the young of closely related types? It scarcely seems probable, though of course it is possible, that this one genus should at that time have had larvæ capable of such wide-spread dissemination. No other cystids apparently have the range of *Echinosphæra*, as no doubt they would have, were larval distribution the only factor. Furthermore, the fact that the projection by which the animal was at one time attached is, in the adult specimens, generally obscure and at times obsolete is positive evidence in favor of a detached existence. That, subsequent to its detachment, the animal did not remain passive is evidenced by the character of the plates, which show no signs of the theca having rested upon the bottom. It is possible that *Echinosphæra* may have crawled on the bottom by means of its brachioles, but this is doubtful, to say the least. The evident slenderness of the brachioles and their probable lack of specialization indicate that they were not fitted to function as ambulatory organs.

Detachment in other many-plated Cystidea.—As we have seen, certain specimens of *Aristocystis*, *Fungocystis* and *Craterina* show clear evidence of attachment to extraneous objects. Such an attachment was not of universal occurrence, however, as an examination of Barrande's (1887) figures plainly shows. From the evidence afforded by these figures one may postulate detachment of the organism, after a period of fixation. Some of the figures indicate that fixation may never have become effective, but one hesitates to draw such extreme conclusions.

As has been indicated above, a marked localized smoothing of the plates and a complete covering of all pore structure may be noted wherever definite fixation obtains. On the other hand, the presence of pores opening outward may, I think, be held as indicating that those plates bearing such pores were not in contact with some extraneous object. It is held by Barrande and Bather that the openings of these canals to the exterior were covered. Bather describes this covering as probably a hard epidermis, but not a truly calcified

epistereom. The functions of such canals, were they covered either by a calcified layer or by a hard, impermeable epidermis would probably at once be destroyed. It seems probable that the exterior of the theca was covered by an integument of some sort, but of such a nature as to render possible communication between the canals and the surrounding medium.

Be this as it may, it is apparent that a covering of these pores by a secondary deposition of stereom may be looked for at the point of attachment of the cystid or in any portion of the theca that may have been in contact with some foreign substance. Hence, where we find canals opening freely to the exterior we may be sure that at that point the cystid was not attached at the time of its death. It is conceivable that pores once closed by a calcified layer might after the detachment of the organism be reopened by a resorption of the covering substance, and so we may explain certain cases described hereafter. Bearing these facts in mind, it is interesting closely to examine the figures of *Aristocystis* as given by Barrande. Some of the more instructive figures are here reproduced on Plate 1.

Aristocystis.—Figures 1 and 7 undoubtedly indicate cementation and show the normal effects of such attachment. Figures 5, 6, 9, and 10 as well as other specimens figured by Barrande illustrate a modification of structure however. It is obvious from the flattened area at the base of the theca that the animal was at one time attached. From the size of the region of contact one may judge that the specimen was affixed until a late stage in its development. Subsequently, it probably became detached. That we are justified in assuming such to have been the case seems to be shown by the structure of the base. The plates show no signs of secondary stereom, such as would be deposited in case of cementation, and the pores are open. Again, the impress of the object to which the cystid was attached is not clearly defined, as it would be were the animal to have been attached at the time of its death, or for some time preceding.

Figures 5, 6 represent a case in which attachment was doubtless had at an early stage in the ontogeny of the animal. Subsequently an eleutherozoic habit seems to have been maintained. There is no basal impress or flattening to indicate that the cystid was at any time affixed to the bottom, but a slight asymmetry and the presence of a definite apical plate point to this conclusion.

Under the name *Aristocystites? subcylindricus*, which he gives as a variety of *A. bohemicus*, Barrande figures a number of specimens which seem in no case to have been affixed. Barrande noted the uniform absence of basal depressions and wrote as follows regarding the material in the explanation of Plate 13:

Les divers spécimens, que nous avons figurés sous ce nom, semblent se distinguer, d'abord par leur forme allongée, arrondie au bout, et ensuite par la disposition des

plaquettes, qui constituent leur extrémité inférieure. Celle-ci ne présente point la cavité simulant une ouverture, que nous avons figurée en divers spécimens sur la Pl. 12, et qui appartiennent au type: *Aristoc. Bohemicus.*

It is to be noted in the case of these specimens that there is no basal depressed area, no marked asymmetry of the theca, and the plates all show clearly defined diplopores. Furthermore, the central apical plate is sometimes wanting, and when present is frequently fused to one of the circumjacent plates of the proximal ring. The plates are tumid, and fixation may only be predicated at a very remote stage in the ontogeny of the animals. *Aristocystis desiratus* figured by Barrande on Plate 20, figures 1 and 2, indicates a very similar condition of affairs.

Craterina.—In the case of *Craterina* evidence of non-attachment similar in all respects to that just given respecting *Aristocystis* might be adduced, although as a rule fixation seems to have been maintained until a relatively later stage in development. In a number of instances the pit indicating the former area of attachment has tubercles over the surface which obviously could not have been present at the time of fixation, and must consequently have been formed subsequent to the detachment of the animals.

Pyrocystis.—*Pyrocystis* likewise furnishes conclusive evidence that in its adult stage fixation was but irregularly effective. A specimen of *Pyrocystis pirum* figured by Barrande (Pl. 29, II, figs. 23, and 24) shows no signs of having been cemented to the bottom. The base of the theca is rounded; there is no impressed area, and the entire surface is quite strongly tubercular. The assumption of freedom by this type is somewhat remarkable in that the general form of the theca indicates a fairly well established statozoic habit. The marked constriction of the lower portion of the theca which is the precursor of a differentiated pedicle or column, and the symmetrical arrangement of the food grooves point most strongly to this conclusion.

Orocystis.—The placing of *Orocystis* in this group rests upon somewhat uncertain evidence. In a view of the basal portion of a specimen given by Barrande (Pl. 7, fig. 15) there is no sign of a point of attachment. Barrande points out this fact, but says "nous croyons reconnaître sa place." Without an examination of the specimen itself it is impossible to determine the status of the form. The chances are, however, that if the point of fixation were so inconspicuous as not to be indicated in the figure, we are safe in assigning *Orocystis helmhackeri* to the eleutherozoic Cystidea. Fixation if effective in such a form, at least in the adult stage, would leave an unmistakable impress on the structure of the organism. Considering the remarkably fine preservation of the material, any evidence of fixation should be at once apparent.

It is not necessary, I think, to cite further cases of freedom in adult stages among these primitive types. A sufficient number of instances have been given clearly to indicate that an eleutherozoic habit was largely maintained among these many-plated, early Cystidea. It may no doubt be safely assumed that this form of life may be postulated for many such organisms. It may well be that in some instances fixation was effective throughout the life of the animals, but it is probable that these form exceptions to the rule.

It is evident that the members of this subgroup do not exactly fall within the limits of Group I as defined. There is no column unless one considers that such be potentially present. It is in this sense that the forms were classified as they are here found. They could not be listed with Group II where the column had been differentiated and subsequently lost, nor well with Group III; and it did not seem best to create a new group for their reception.

This subgroup is of great interest as containing the first variants from an attached existence. As has been elsewhere noted, the assumption of an eleutherozoic existence by these forms is less in the nature of an abandonment of a statozoic habit as an imperfect acquirement of such a form of life. For this reason these types may be held as truly intermediate between the primitive eleutherozoic stock and the primitive statozoic forms. It by no means follows that these genera are the actual progenitors of the more typical Pelmatozoa, but nevertheless they indicate the stages through which such ancestral types may have passed.

These forms are likewise of great interest as showing that even when the tendency toward a statozoic existence had its inception, a time the tendency should be perhaps in greatest force, reversion to an eleutherozoic habit should have obtained. This shows how vitally the eleutherozoic habit had impressed itself upon the pelmatozoan stock. It is not surprising therefore that in the later forms, when the force of this tendency toward fixation should have somewhat spent its strength, that the assumption of a free existence should have become almost universally effective.

It is somewhat difficult to determine what form of life must have been led by the Cystidea referred to this subgroup. As has been shown in the cases cited above, there is apparently no indication of the animals having rested upon or in contact with any extraneous object. Such being the case we must postulate an existence of such a nature as to render the organisms quite free from contact with the bottom, or else to admit of free motion along the bottom as among the bottom-crawling Holothurians.

As has been argued above in the case of *Echinosphæra,* it seems quite possible that this form at least was freely floating. It may be that in such a case the brachial appendages, feeble though they are,

might be of considerable assistance in determining slight movement. Many of the other forms referred to this group, from the considerable weight of their thecal plates and the generally cumbrous aspect of the body, seem not to be equally well fitted for a pelagic habitat, however. On the other hand, it is impossible to ascribe a sessile form of life to these organisms for the reasons given above.

If a free swimming existence be barred in such cases we have the alternative of comparatively free motion upon the sea bottom. Owing to the rather feeble nature of the brachial appendages one may not consider them as capable of functioning to any considerable extent as ambulatory appendages. In some cases, as in *Protocrinus*, where pseudo-ambulacra are well developed there is a possibility of structures comparable in a degree to the podia of the Echinoidea having been present. Even in the case of the *Diploporita* where numerous vertical canals perforate the thecal walls, it is perhaps not inconceivable that organs of a similar function may have been present. The diplopores themselves in certain cases may have harbored such specialized organs. This hypothesis is not as improbable as it may sound at first. We know that in the earliest echinoids such as *Bothriocidaris*, podia or organs of similar function must have been present. Such a form we may only conceive to have been derived from a line of these many-plated cystids. The chances are, therefore, that podia should be represented in these ancestral forms by similar or equivalent organs. Certain it is that we must postulate organs of locomotion of some sort in the very early common eleutherozoic ancestor of the Echinoderma. Lacking brachial appendages what could be more natural than that some such sort of ambulatory organs should have been present? Upon the assumption of a purely statozoic existence by certain lines of this primitive stock, such organs would in time become eliminated through disuse.

There is an interesting structural feature which is apparently intimately associated with the assumption of a statozoic existence by these many-plated cystids. This is the presence of a definite central apical plate. It is needless to more than mention the lengthy discussion that has been carried on in regard to the origin and homologies of such a plate. Its significance in this particular group of organisms alone will be discussed at this time.

It is to be noted in the case of all figures of the bases of these cystids where the sutures of the plates are visible, that there is a well-defined apical plate surrounded by a ring composed of a variable number of plates. This apical plate seems in all cases to be the center of the area of attachment. One may infer that attachment was had primarily by means of this plate alone. Whether this plate represents a definite skeletal element of any morphological significance is a question difficult of solution. I believe it does not.

Fixation may have become effective so early in the ontogeny of such cystids as to have preceded the formation of a definite skeletal structure. If such were the case attachment would take place at the aboral pole irrespective of plate orientation. Under such circumstances it is obvious that at the point of fixation a plate would be formed, and that the circumjacent plates would of necessity assume a somewhat definite arrangement. Even had fixation occurred subsequent to the formation of definite skeletal elements, it is apparent that the point of cementation must have been a plate, and that this plate must necessarily be located somewhere near the aboral pole. Subsequent to the attachment of the animal, a readjustment of the plates of the basal portion of the theca must have taken place, which would give the proximal ring as we find it. The apparently variable location of the point of fixation seems to preclude the possibility of cementation constantly taking place through the agency of a definite plate.

According to this hypothesis then, the formation of the central apical plate is a secondary matter and entirely dependent upon the fixation of the animal. It may well be that in the phylogeny of the Pelmatozoa this plate might acquire a certain fixed status and be perpetuated as a definite element, perhaps homologous to the terminal ossicle of the pentacrinoid stem of *Antedon*.

CYSTIDEA, TYPE 2.

This group, as opposed to the preceding, consists of Cystidea which have well-developed columns. It is probable that all of the forms here referred were freely moving organisms, during the greater part of their lives at least. Some maintained an erect position, while in the case of other forms we note a tendency toward the assumption of a prostrate habit. This tendency becomes more marked and reaches its maximum development among those forms referred to the next subgroup. The column in all cases probably functioned merely as an organ for temporary attachment. Attachment in this group was apparently never by means of radicular cirri, and seldom by cementation. In the majority of cases the distal portion of the column seems to have been more or less prehensile and it is probable that anchorage was effected by looping this portion of the stem about some stationary object. In all these forms the entire stem appears to have been quite flexible.

Structure of stem in type 2.—The columns possessed by such Cystidea, with the exception of the most primitive types, are essentially similar in structure. The columnals are circular and are of large size next the theca. Distad the diameter of the column decreases rapidly. After a certain point, where the stem is comparatively slender, the column continues to taper, but at a greatly diminished

rate. Measurements of the stem of a *Pleurocystites filitextus* will illustrate these features admirably. The specimen is an unusually large one, and the stem as preserved measures 70 mm. in length. Probably not more than 5 or 10 mm. of the stem is wanting. Possibly the column is essentially complete.

The proximal columnal measures 6.1 mm. in diameter and the most distal columnal preserved 1.2 mm. The stem tapers most rapidly in the first 16 mm. where it decreases from 6.1 to 4 mm. in diameter. Distad from this point the rate of decrease is lower and comparatively uniform. The proximal 16 mm. of the stem consists of short sharply annulated columnals. Distad there is a gradual transition from the short ossicles to comparatively long subcylindrical columnals. These soon reach their maximum length which in this species is 2 mm. Continuing, the ossicles rapidly become smaller and smaller, their length in some instances being a trifle greater than their breadth.

The proximal, rapidly tapering portion of the columns in these forms has a remarkably large central perforation. This seems to be less in the nature of an axial canal than a cavity for the reception of a portion of the visceral mass. Again, it may well be that this cavity lodged the musculature which largely controlled the movement of the column. If we assume the degree of movement that seems to be indicated by the structure of the columns of these forms, we must assume a corresponding high development of muscles to bring about such movement. Such a musculature could not be contained within the narrow confines of the average axial canal. As a result of the large size of the perforation, the walls are thin and this portion of the stem is frequently found considerably flattened. A feature which is not specially noticeable in *Pleurocystis* but which is strikingly shown by *Cheirocrinus* is the mode of articulation of the columnals in this portion of the stem. The arrangement is such that great freedom of motion is possible.

Type of life led.—As indicated above, some of the members of this group maintained an erect position, while others were prostrate. The second type was probably derived from the first, and represents a divergent off shoot comparable in mode of life to Type 3 among the Cystidea, and such a form as *Eleutherocrinus* among the Blastoidea. There is apparently no parallel case among the Crinoidea. It is to be expected that the different genera referred to one of these divisions will partake to a greater or less extent of the nature of the other. A typical prostrate cystid is *Pleurocystis* while *Glyptocystis* may be chosen as an example of the other division.

Detachment among the erect, stalked Cystidea.—The evidence afforded by the erect types as to the maintenance of an eleutherozoic habit is as a rule inconclusive, but yet convincing. It is probable that a

very large proportion of the stalked Cystidea not included in Type 3 or not otherwise disposed of in the present group may be held as erect, detached forms. Among the more primitive Cystidea, particularly, it seems highly probable that permanent fixation was of comparatively rare occurrence. It is among these more simple types particularly that we are able conclusively to prove nonfixation, for here we have complete columns more frequently preserved. Among the later and more specialized cystids the structure of the column and its marked flexibility, which is frequently made more apparent through a looping of its distal portion, indicates anything but adaptation to a purely statozoic form of life. Wherever the type of column heretofore described as generally typical of the greater number of forms referable to this group is found, I think we may be safe in assuming an eleutherozoic habit.

Arachnocystis.—The most primitive type that may be assigned to this subgroup is *Arachnocystis*, a genus with the highly interesting *Echinosphærites infaustus* of Barrande as the genotype. In this form we have one of the most rudimentary columns known among the Pelmatozoa. In other genera we have evagination of the body wall and marked constriction of the basal portion of the theca, but here is to be found the simplest column that may be called such with justice. In *Arachnocystis* we find that the column has been differentiated to the extent of being composed of a regular vertical series of imbricating plates therein differing from a mere evagination of the thecal wall. Figures 5, 6, Plate 2, give a fair notion of the structure of the column. From the figures given, there appear to be five rows of plates, but according to Barrande (1887, p. 28) there may be five or six ranges. The column is in most cases of marked brevity, none figured exceeding a length of 50 mm. There is in no case where the distal extremity is preserved any indication of attachment by the organism.

The column of *Arachnocystis* must have differed functionally as well as structurally from that of the more specialized members of this group. Although mobile to a certain extent, the column of Arachnocystis was not sufficiently slender nor properly constructed to function as a prehensile organ. Subsequent to the assumption of an eleutherozoic habit, which obtained during the adult stages of the animals, such a column could not have been other than a hindrance. The sole service it could render the cystid would be as a sort of ballast. Considering the relative insignificance of the column compared with the bulk of the theca, this function must have been of inconsiderable consequence.

It is evident that this genus has been derived from a type not greatly dissimilar to *Echinosphæra*. The slight protuberance to be noted in that genus has, however, been considerably accentuated.

It seems probable that in these forms attachment was had in the young stages by a central apical plate. Continued fixation eventually caused a considerable constriction of the lower portion of the theca even though attachment did not continue throughout the individual lives of the animals. This condition of affairs has already been noted in the case of *Pyrocystis pirum*. A continuation of the process would eventually result in a definite orientation of the plates comprising the pedicle, and a further differentiation of this portion of the animal.

In *Arachnocystis* is to be noted a very considerable development of the brachioles. These are fairly stout, and apparently have a length of at least twice that of the theca. They are biserial, and either two or three are borne by an individual. Taking into account the probable buoyancy of the animal, it is not inconceivable that these brachioles might have constituted fairly effective swimming organs.

The high interest that such a form holds is due in no small part to the continued activity of a tendency in modifying an animal, even though the conditions of life for which the modifications are fitted are but imperfectly and irregularly effective. A more extended discussion of this topic will be given in a subsequent portion of the paper.

Ascocystis.—In the remarkable genus *Ascocystis*, we have indubitable evidence of the nonattachment of the organism. The column is extremely short, being but a fraction of the length of the theca. It tapers rapidly and apparently ends in a point. There is absolutely no evidence of fixation. This genus is equipped with a large number of brachial appendages which completely encircle the distal portion of the theca. It seems quite reasonable to expect that with its considerable development of brachioles the genus may have been well adapted to a free-swimming existence.

Macrocystella.—Among the earliest of the forms referable to this group, though by no means the most simple, is the curious genus *Macrocystella* which might better perhaps be described as a tricyclic crinoid than as a cystid. Figure 7, Plate 2, copied from Bather gives a reconstruction of this remarkable Upper Cambrian genus. As may be seen, the distal portion of the column is quite slender, and it seems probable that it was used to loop about some stationary object. The characters of the stem agree in all essential respects with those given as typical of the majority of the members of this group.

In connection with the eleutherozoic habit of this type is to be noted the total absence of a column in the case of *Lichenoides*, a genus probably closely allied to *Macrocystella*, and referred to the same family by Bather.

Glyptocystis.—In the case of *Glyptocystis* a detached existence is predicated largely on the basis of the column structure. It is to be

noted that this is one of the few genera to which an eleutherozoic habit has been ascribed by former writers. The column is of the type given as characterisitic of the members of this group, and there is no evidence of fixation. In addition to the figures given in various publications I have personally examined and collected a considerable number of beautifully preserved specimens referable to this genus, and in no case have found any evidence of a terminal plate or other structural modification for purposes of attachment. The column is in many instances remarkably short, scarcely exceeding the length of the theca. Probably in no case was it of more than twice the length of the theca. It tapers quite rapidly, and gives evidence of having been unusually flexible.

In *Glyptocystis* the negative evidence of the lack of special adaptation to a prostrate mode of life points strongly to the conclusion that in this genus an erect position was constantly maintained. This fact argues against the derivation of *Glyptocystis* from *Cheirocrinus* as has been suggested by Jaekel, inasmuch as in the latter genus are to be noted marked modifications pointing to the assumption of a prostrate habit.

Lepadocrinus.—The genus *Lepadocrinus* with its curious column is worthy of special mention in connection with this group. In this genus a considerable number of the distal columnals are fused to form an elongate subcylindrical body. (Pl. 5, figs. 6, 7.) There are no signs of cirri, and the distal end of the column is smoothly rounded off. Subsequent to the fusion of the columnals there was a secondary deposition of stereom, causing a marked enlargement of this portion of the column. The resemblance of this fused portion, barring the lack of modified cirri, to "*Ancyrocrinus*" is worthy of note. It seems quite possible that in this instance, as in the case of the crinoid, the fused appendage served as ballast or as a drag. It may be that the distal portion of the column in *Lepadocrinus* was buried in soft mud, but if such were the case fixation must have been of a most precarious sort. Attachment by cementation apparently never took place. It is of particular interest to note an eleutherozoic habit in the case of *Lepadocrinus*, inasmuch as this was the last known representative of the erect, stalked Cystidea.

Evidence of a prostrate habit in type 2.—In many of the genera probably referable to this group we know little or nothing regarding the structure of the column. Owing to this fact we may not with certainty ascribe an eleutherozoic habit to them. It is not until we come to treat of those forms in which the modifications incident to the assumption of a prostrate existence become manifest that we may safely postulate a free existence from the evidence afforded by the theca alone. These changes are, if well developed, unmistakable and of necessity infallibly point to a detached existence.

The more obvious features to be noted are: The acquisition of a marked asymmetry, the theca being differentiated into an upper and a lower surface; the localization of pore-rhombs on one (the upper) surface; the atrophy of certain food grooves; and finally the shifting of the anal opening to the extreme proximal portion of the theca. These features may be present in varying degrees, and are usually accompanied by characterisitic minor phenomena. It is to be noted that these modifications are even more characteristic of those forms constituting type 3. There, however, the same results are often attained by different methods.

Dendrocystis.—In *Dendrocystis* we have a very primitive type which may well be referred to the prostrate division of this group. A close comparison of the figures given by Barrande shows that we may differentiate between an upper and lower surface of the theca. Moreover, the anal aperture has been carried well backward, and is situated in the extreme proximal portion of the theca.

But a single brachiole is borne by the animal. This is remarkably stout, and doubtless served in the propulsion of the animal. It has been considered by Barrande and others that this organ is a closed tube. Bather, on the other hand, believes that a ventral groove was present, which is as a rule closed by the apposition of the lateral rows of plates forming the brachiole. It seems highly probable that the latter view is correct.

The theca of *Dendrocystis* is composed of a great number of irregularly arranged plates. Nevertheless it seems possible to distinguish an upper and lower surface. Barrande's figures indicate rather diverse structural conditions, which may be due to actual variation within the species, or, what seems fairly probable, to the fact that there are two species represented. For this reason and because of the fact that I have been able to examine but indifferent original material, I am unwilling to draw other than tentative conclusions in regard to the form.

The column in its proximal portion is made up of a great number of irregularly arranged plates. Distad the plates become larger, and a more definite arrangement is to be noted. The greater part of the column is slender and composed of a double series of elongate, alternating plates. This arrangement indicates a considerable degree of flexibility. Such a column could not have been effective other than as an organ by which temporary attachment might be had through the looping of its distal portion about some stationary object.

Before discussing the typical prostrate form *Pleurocystis*, attention should be called to a few genera that show a more or less clearly defined tendency toward the assumption of such a form of existence.

Such types are *Erinocystis*, *Amygdalocystis*, and *Cheirocrinus*. All these cystids may be held as eleutherozoic forms, and the further assumption of a partially perfected prostrate habit rests largely on the evidence of such structural modifications as have hitherto been cited as characterizing such a form of life.

Amygdalocystis.—*Amygdalocystis* has an unusually short and feeble column which generally gives evidence of having been looped. The probable proximal ancestor of the genus, which is as yet undescribed, is a subcylindrical form with three food grooves. The flattening of the theca and the atrophy of one of the food grooves, as well as the nature of the column, seem to point to the assumption of a prostrate form of life. One has difficulty in explaining such a compression of the theca on any other basis. A spherical or subcylindrical type, if an erect position be constantly maintained, will tend to give rise to a line in which the radial symmetry is made more and more perfect. The almost equal convexity of the two sides, as shown in *Amygdalocystis* and *Platycystis*, would seem to indicate at least that the animal did not constantly rest on one side, even were a prostrate condition maintained.

Erinocystis.—This tendency toward the assumption of a prostrate condition is quite marked in the small group to which Jaekel has given the name *Erinocystis*. This genus was short-lived and apparently left no descendants. *Erinocystis* illustrates modifications which are of considerable interest in that they differ in a marked degree from those to be observed in the other types to be discussed.

In such a form as *Erinocystis volborthi*, Plate 2, figure 3, a marked asymmetry is to be noted. One side of the theca is decidedly flattened. The lower flattened side of the theca is well shown in figure 8, Plate 2, which illustrates a closely allied type, *Echinoencrinus angulosus*. The anal opening has been carried outward and backward to a marked degree and is situated at the end of an extraordinary projection of the theca formed by the hypertrophy of certain of the calycal plates. This lateral backward extension of the thecal plates is especially to be noted in the case of *Erinocystis angulata*. The column, as may be seen in Plate 2, figures 3, 8, is of the general type characteristic of the group as a whole.

Cheirocrinus.—In the genus *Cheirocrinus* we find imperfectly developed the same general modification to bring about a flattening of one surface of the animal that is to be noted in *Pleurocystis*. This flattening, instead of being acquired through the readjustment and modification of plates already present in the theca, is obtained through the excessive multiplication of circum-anal plates. If this multiplication of plates be continued, it is obvious that one side of the theca will in time largely be composed of such

plates. Such is the case in *Pleurocystis*, where the definite skeletal elements are restricted mainly to the upper surface and extend below as a rule only as marginals.

In *Cheirocrinus* this process has not been carried so far, but in such a form as *Cheirocrinus penniger* (Pl. 2, figs. 1, 2) it is to be noted that there is an appreciable flattening of the theca and a remarkable enlargement of the circum-anal area. *Scoliocystis* seems to show an intermediate stage in the evolution of this type of structure, comparable in degree with that shown by *Cheirocrinus walcotti*.

Pleurocystis.—Pleurocystis undoubtedly led an eleutherozoic existence, and one, as elsewhere suggested, quite at variance in certain respects with that to be found in the case of most of the detached Pelmatozoa. All the structural evidence afforded by the genus points clearly to the assumption by the form of a purely prostrate habit. For this type of life *Pleurocystis* is only excelled in the perfection of its adaptation by the members of the next subgroup, which doubtless represent the constant assumption of this sort of existence for a long period of time.

An examination of specimens of *Pleurocystis*, or even of figures, such as figure 4, Plate 2, and figure 3, Plate 3, will clearly show the extent of these modifications. The marked asymmetry of the genus which can only be accounted for on the basis of the assumption of a prostrate habit, is a most peculiar and striking feature. One notes the extreme flattening of the anal (ventral) side and the strong convexity of the antanal side; the atrophy of all but two of the food grooves; the location of all the pectini-rhombs on the dorsal convex side; the extreme posterior location of the anal opening; the fact that the column is constantly coiled in the same plane as that of the flattened theca; and other characteristic features. All these facts point to the same conclusion.

A free or semifree type of existence could be of little benefit to an animal were it not for the possession of organs of locomotion. Possibly the brachioles of *Pleurocystis* might have been used in somewhat the same manner as the flagellæ of certain Protozoa. By a lashing or rowing motion of these organs it is quite conceivable that locomotion might have been effected. The brachioles are too long, slender, and flexible to function as ambulatory appendages, but they may have caught the bottom laterally and in this way have served as organs of propulsion. The column in this group probably in no case helped give impetus to the animal's movements as seems to have been the case in the next subgroup.

The column of *Pleurocystis* is comparatively short and quite stout in the proximal portion. Distally it tapers rapidly until it becomes remarkably slender, Plate 3, figure 3. The distal two inches or so of

the column are, in all cases that have come under my observation, somewhat coiled. In two or three specimens that I have examined there could scarcely have been more than half an inch of the distal portion of the columns lacking. Possibly the stems were complete. In no case was there the slightest trace of rootlets, and no evidence of a distal basal expansion such as is common among the Crinoidea. The evidence seems to point to the conclusion that *Pleurocystis* was never firmly rooted to any one spot but anchored itself by hooking the tenuous distal portion of its stem about some extraneous object.

The analysis of the theca and the figures of *Pleurocystis* as given by Jaekel and Bather are inaccurate in several important features. Plates 1 and 4 as given by them should be split vertically and portions united with 2 and 3. Plate 13 is not present in the cup, the apophyses of Plates 12 and 14 uniting without the intervention of another plate. This plate was present in very primitive types but was crowded out subsequently. A full discussion of this subject will be given in a paper which treats in detail of the Pleurocystidæ. In the present paper it was thought best rather to illustrate an actual specimen than to give a reconstruction. It will be noted that the structure of the column is quite different from that given by either Bather or Jaekel.

The marked asymmetry of *Pleurocystis* is unquestionably secondary. What the ancestral erect cystid was like is an interesting question. Bather, in Lankester, derives *Pleurocystis* from *Cheirocrinus* and places both genera in the subfamily Glyptocystidæ. I am personally inclined to derive *Pleurocystis* from a form having essentially the structure of *Echinoencrinus*. This genus is not the ancestor of *Pleurocystis*, but both were probably derived from a common ancestor not far removed.

CYSTIDEA, TYPE 3.

We have here probably the most aberrant type of evolution to be found among the Echinoderma, and one which in the nature of things, one would least expect. To find among the Pelmatozoa a group of organisms that are perhaps more highly specialized for purposes of locomotion than a large proportion of the Eleutherozoa is a novel experience. So unlike Echinoderms are they in certain respects that some of them have been described as Crustacea, which indeed they closely simulate. The members of this group moved actively over the bottom, using both column and "brachioles," when present, as organs of locomotion. In this regard, they may be looked upon as going a step beyond that reached by type 2, and are closely comparable to *Eleutherocrinus*. The departure from the beaten path seems to have been quite successful, for these types range from the Cambrian to the very latest cystid appearance in the Devonian (Oriskany).

There is a general unity of structure among these forms that strongly argues for a monophyletic origin of the group. In all, the theca is flattened on one side and more or less highly arched on the other. The theca is elongate and comparatively narrow. The stem is large in the proximal portion and tapers rapidly distad. It is short and composed of a double row of curiously imbricating ossicles Plate 3, figures 1, 5, 6—a feature which gives the column great flexibility. The brachioles when present are two in number and comparatively slender, reminding one strongly of the jointed appendages of the Crustacea. No pore-rhombs are present. A more detailed description of the structural features which characterize the group will be found under the discussion of the different genera.

In the discussion of this subgroup a somewhat unusual treatment will be accorded the forms. Owing to the remarkable modifications exhibited by the members of the group and the evidence of their having lived quite differently from the majority of the cystids, it has been thought best to treat of the best known and more specialized forms first. *Anomalocystis* as representing the terminal member of a highly specialized line, necessarily possesses the most striking adaptations to the form of life which had been assumed by the group as a whole. For this reason it is possible to predicate with a fair degree of certainty the habits of the animal. Whatever type of life obtained in the case of *Anomalocystis* we may be fairly sure was possessed to a certain degree by the other forms referred to the group. Furthermore, by taking the most complex form first, we may note its modifications and trace more or less perfectly the steps by which they were brought about.

Anomalocystis.—The genus *Anomalocystis* was founded by Hall (1859, p. 132) with the Helderbergian cystid *A. cornutus* as genotype. In the same volume he refers another species *disparilis*, from the Oriskany, to the genus. As a matter of fact the generic description as given by Hall is based upon both species. Bather in Lankaster, refers *cornutus* doubtfully to *Ateleocystis*, Billings, and *disparilis* to *Placocystis*. Were *Anomalocystis* and *Ateleocystis* proved to be the same, it is doubtful which name should hold. According to the date of publication, it seems that *Ateleocystis* had precedence. Billings himself, however, in describing the genus (1858, p. 72) says: "Should it be ascertained hereafter that the two genera are identical, this species must be referred to *Anomalocystis*, which has the precedence." In this case, Hall had sent out advance sheets containing a description of the genus, which antedated Billings's publication. If these advance sheets are to be recognized, the date of *Anomalocystis* must be shifted back a year or more.

It may be held, I think, that *A. cornutus* and *A. disparilis* are congeneric. Indeed there is no good reason why the later type

should not have been a lineal descendant of the earlier Helderbergian form. I have examined a very considerable series of both species and although as a rule the specimens of *A. cornutus* are in an unsatisfactory state of preservation I feel that this is a safe assumption. Furthermore it may be, as is held by Bather, that *disparilis* and the forms referred to *Placocystis* are congeneric. I personally feel that this is not the case, there being sufficient difference in the arrangement of the plates to warrant a generic distinction being made. *A. cornutus*, on the other hand, I feel quite certain is distinct from *Ateleocystis*. If this be the case and if *cornutus* and *disparilis* be congeneric *Placocystis* must of necessity fall into synonymy with *Anomalocystis* providing Bather's stand be well taken.

The following description is taken mainly from *A. disparilis* of which figures are given on Plate 3, figures 9 to 11. *Anomalocystis* has an elongate theca highly arched on one side, and flattened-concave on the opposite side. The distal portion of the body is less highly arched and broader than the proximal. Lying on the flat side, without any appendages, the whole body slants downward toward the distal end.

It is to be noted that lying in its natural position, the greater portion of the lower side does not come in contact with the surface upon which the theca rests. Rather the body rests upon the downward produced edges of the theca, which act as runners. In *Placocystis*, Plate 3, figures 1, 2, an interesting variation is to be noted. Here the body is raised above the bottom by means of a central, longitudinal keel, which passes well forward from the base of the theca. There are apparently no lateral produced edges. These runners are of obvious advantage in minimizing the amount of friction to be overcome by the animal in pushing along over the sea bottom. It is to be noted in the case of *Anomalocystis* that the lateral keels are most strongly developed in the posterior portion of the theca, and it is largely due to them that the body is given the forward tilt that is so noticeable when a specimen is laid upon a flat surface.

The anterior (distal) portion of the theca presents structural features not paralleled in any other group of the Cystidea. The body terminates rather abruptly, and in the face thus formed there is to be found an elongate opening. This opening is oblong, with the long axis parallel to the flattened base of the theca. The opening is but a trifle less than one-half the breadth of the anterior end, and is approximately twice as broad as high. It seems possible, as will be subsequently pointed out, that this terminal aperture harbored both the mouth and anal opening. The margin of the theca below the mouth projects somewhat forward, this projection being largely formed by a median plate on the bottom of the theca. This plate is better developed and possibly was of great importance to the

organisms among the older representatives of the Anomalocystidæ. In the dorsal surface of the theca the margin projects but slightly over the terminal aperture. In some cases it is practically flush with the opening. Laterally the margin is considerably extended, forming an appreciable overhang. This invagination of the margin for the length of the aperture is quite marked.

There is a very interesting structure connected with the thecal opening that has apparently not hitherto been observed. This is a sort of trapdoor or flap that depends from the upper margin of the opening. The composition of this flap may not be determined with certainty. In two specimens where preserved it is somewhat raised, and projects beyond the margin of the theca. It maintains its shape, which is that of the aperture, perfectly. This fact and other evidence relative to the hinging of the structure would make it appear that we have to deal with a solid plate. This may have been formed by the fusion of a number of small plates, however.

It is evident that the function of this plate was to close the terminal aperture. On the lower surface of the plate and running longitudinally across it near the outer margin, is a pronounced ridge. When the plate is dropped this ridge rests on the inner floor of the opening. The portion of the plate anterior to the ridge fits over the lower margin of the theca, and the opening is tightly closed. The invagination of the margin above the opening seems not to be without a reason, for if the margin projected uniformly across the anterior end it would be impossible for this plate to be completely raised.

The mechanics of the operation of this plate are comparatively simple. A specimen from which the dorsal surface has largely been removed shows the interior of the distal portion of the theca quite clearly. On either side of the opening is a process which extends to the top of the aperture. On these processes the plate was no doubt hinged. On the floor of the theca are two deep longitudinal pits. These probably served as the points of attachment for the muscles that raised and lowered the plate.

The lateral appendages of *Placocystis* and *Anomalocystis* are a peculiar and special modification. By Haeckel (1896, p. 40) they have been restored in the case of *Placocystis* as true brachioles. Bather (1900) considers that such an appendage "may have served as an arm, i. e., as the bearer of a tentaculate extension of the water system, and of a ciliated path to the mouth." So far as may be observed, these appendages show no signs of being jointed, and in the case of *Placocystis*, on the authority of Bather, may reach a length of two-thirds that of the theca. In *Anomalocystis* the appendages seem to have been considerably shorter. The spines, as Bather styles them, are somewhat curiously articulated at the distal angles of the theca.

Each of these appendages, I believe, may be looked upon as a modified marginal plate. The spine has no communication with the interior and the musculature which controls its movements is external. The muscles were doubtless lodged in the lateral, somewhat depressed areas on either side of the terminal opening. The spines, as I shall subsequently point out, almost certainly had no other function than to raise the adoral portion of the body. It seems possible, further, that they may have functioned to some extent as ambulatory organs.

The structure of the column is but imperfectly known. It apparently is not essentially different from that possessed by other members of the group, however. It is composed of two longitudinal series of ossicles. In the proximal portion of the column there seems to be a semifusion of the apposed half-segments, resulting in the formation of complete rings. That this fusion has been but imperfectly acquired is shown by an individual in which the column is broken. In this case the line of fracture clearly indicates the original longitudinal division of the stem. The column in its proximal portion is of large size, but apparently tapers rapidly distad. The stem ossicles are remarkably thin and this gives the column a relatively enormous central perforation. This cavity probably lodged the muscles that controlled the movements of the column.

The articulation of the column with the theca is of considerable interest. It is to be noted, as shown in figure 11, plate 3, that the cavity within which the proximal portion of the column is lodged is quite deep and socket-like in its conformation. All available evidence points to unusually free motion of the column within this cavity, both laterally and vertically. Taken in conjunction with the great flexibility of the column itself, and the evidence of a highly developed musculature, it is evident that the stem was capable of a great range of movement. All these facts point strongly to the conclusion that the column had very special functions, quite different from those normally assigned to the pelmatozoan stem.

A brief discussion of the habits of this type as they are believed to have been will illustrate clearly the probable functions of the various parts and the reasons for the modifications to be noted in the gross structure of the organism. It is believed that the animals propelled themselves along the bottom by means of their column. This was pulled forward, elevating the posterior portion of the theca; pressure was then exerted which drove the animal forward. It is here that we see the probable use to which the anterior appendages were put. With the posterior portion elevated and a forward pressure applied it is obvious that the tendency would be to drive the adoral part of the animal into the sediment of the bottom. However, were the anterior appendages to be slightly drawn inward so as to elevate the anterior portion of the theca somewhat above the

bottom, this forward movement would result simply in sliding the animal along the bottom instead of burying it. While in motion it is probable that the flap, which has been described above, was pulled down. This covered the anterior opening and prevented the intrusion of undesirable matter.

The feeding habits of *Anomalocystis*, as indicated by the structure of the animal, seem to be peculiar to itself and the associated forms referred to the subgroup, at least among the Pelmatozoa. Lacking food-gathering appendages, it is obvious that food must have entered the mouth directly. It seems highly probable that when feeding, the terminal aperture was kept open and the animal without elevating the adoral portion of the theca pushed itself along the bottom. By this process the cystid could fill itself with bottom ooze, in which its food was contained.

Trochocystis.—*Trochocystis*, which may be considered the most simple known type and perhaps constitutes the radicle from which sprung the remaining genera of the group, is a Cambrian genus described by Barrande. The various interpretations of the genus given by Jaekel (1901), Haeckel (1896), and Bather (1900), are so diverse that one with no more evidence than is afforded by figures alone feels a considerable degree of hesitancy in coming to any definite conclusions regarding the form. This is unfortunate, for upon the correct interpretation of this genus depends to a great extent one's ability fully to comprehend the origin of certain structures to be found in the later types. The uncertainty relative to the structure of *Trochocystis* is to a great part due to the preservation of the specimens, which occur largely as molds, and as such they have been figured. The difficulties attendant upon the elucidation of such material are very great, and are almost insuperable when one has but figures to deal with.

In *Trochocystis* we find the theca flattened, indicating the assumption and probably fairly long maintenance of a prostrate existence. The two surfaces of the theca are composed of a great number of polygonal plates which are surrounded by 12 comparatively massive marginal plates. A dorsal and ventral surface may apparently be distinguished, both through the relative number of plates comprising the two sides and by the relative extent to which the marginals take part in the structure of the two areas. Aborally the marginals pass insensibly into the column, which is composed of a double alternating series of plates. (Pl. 3, fig. 5.)

It is probable that the stem in *Trochocystis* was far less specialized in function than the equivalent organ in later forms. Owing to its structure, considerable freedom of lateral movement was made possible, but even this is due to the flexibility of the column itself. There was but little or no play at the junction of the column with

the theca. As a result, the possibilities of vertical movement were far more limited than in the case of the later types. It seems reasonable to expect that even in *Trochocystis* the column performed no slight service in the propulsion of the animal. If Jaekel (1901) be correct in assuming the presence of marginal ambulacral structures it might follow that movement was to some extent performed by brachioles or their equivalents. The presence of food-grooves in this type I feel is far from proved, however.

In numerous figures given of *Trochocystis* by Barrande (1887) is to be noted a curious central distal plate, of which an enlargement is here given on Plate 3, figure 4. This plate is at times extended beyond the theca, and at times folded down apparently covering the central anterior aperture. The structure of this plate and its apparent relation to the theca at once suggest a function similar to that of the hinged plate described in the case of *Anomalocystis*. It seems probable indeed that we are here dealing with homologous structures. If such be the case, the surface to which the plate is hinged in *Trochocystis* corresponds to the dorsal side of *Anomalocystis*.

Concerning the terminal openings of *Trochocystis* but little can definitely be said. There certainly is a central aperture corresponding essentially with that of later types. Barrande (1887), Haeckel (1896), and Bather (1900) state that there are two other openings, one on either side of this central aperture. Jaekel (1901) admits of but one other opening, to which he claims the ambulacral grooves run, thus proving it to be the mouth. Doubtless the question will not be settled until someone makes satisfactory impressions from external molds. It would seem more reasonable on the whole to consider the central opening the mouth, although this view is at variance with the stand taken by former writers who have presumably had an opportunity to study good material.

Mitrocystis.—In *Mitrocystis*, Plate 3, figures 6–8, is to be found a type intermediate in structure between *Trochocystis* and the later genera of the group. In all essential details the genus approximates more nearly to the later forms than it does to *Trochocystis*.

There is to be noted a marked differentiation into an upper (dorsal) and a lower (ventral) surface. In the ventral surface there has been a very considerable consolidation of the plates, the number of those inclosed in the circumference of the marginals numbering but a half dozen at most. The dorsal surface is still composed of numerous irregularly arranged plates, although they are fewer in number than in the case of *Trochocystis*. Bilateral symmetry in respect to a vertical longitudinal plane is as yet scarcely appreciable.

Perhaps the most notable structural difference between *Mitrocystis* and *Trochocystis* lies in the fact that *Mitrocystis* has but a single terminal aperture, therein agreeing with the Silurian and

Devonian genera. The uncertainty that obtains relative to the nature of the openings of *Trochocystis* has been noted above. Whatever be the structure in that genus, it is quite certain that we have here an aperture that represents the confluence of the openings of *Trochocystis*, if, indeed, there be more than one. It is interesting to observe the presence of the central, hinged plate in the case of *Mitrocystis*. In Plate 3, figure 8, which represents the under (inner) surface of the plate, there are to be noted several longitudinal ridges. The grooves between these ridges may well represent the points of attachment for the muscles that move the plate.

The column of *Mitrocystis* seems to be in all essential regards quite similar to that possessed by the later genera referable to the Anomalocystidæ. Bather (1900, p. 51) describes it in part as follows: "Stem of about four alternating rows of plates, often provided with thorn-like processes." Barrande's figures do not seem to justify this portion of the description. The column apparently is composed of the normal, double row of ossicles, which seem to be apposed in many cases instead of alternating. In some instances indeed partial fusion seems to have taken place, such as has been described in the case of *Anomalocystis*. The thorn-like processes described by Bather are supposed to be shown in Plate 3, figure 6, which is copied from Bather (1900), who in turn copied it from Barrande. These processes, I believe, are more apparent than real, and are due to the preservation of the specimen rather than to the actual structure of the column. Other specimens illustrated by Barrande show no signs of such spines and agree with allied genera in this regard. It is evident, I think, that in the case of this specimen the substance of the plates has been removed and the processes, if they represent anything, are ridges of ferruginous matter deposited by infiltration in the stem cavity and between the segments.

The articulation of the column with the theca in *Mitrocystis* represents a decided step in advance over the structure shown in the case of *Trochocystis*. There is apparently a fair invagination of the proximal portion of the theca for the reception of the column, and the stem may well have had considerable freedom of motion both in a horizontal and vertical direction.

General discussion of type 3.—There are several other genera referable to this group, but inasmuch as they exhibit no special modifications of structure other than those shown by the forms described, it has not been thought best to include them in the present discussion.

The essential unity in structure shown by the genera referred to this group is notable and argues strongly in favor of their monophyletic origin. Derived no doubt, as suggested by Bather (1900), from a form not widely dissimilar to *Aristocystis*, a prostrate habit of life was early assumed and constantly maintained. In consequence the

changes to be observed in the evolution of the group all tend in one direction—toward the perfection of the type for a prostrate, eleutherozoic life.

There is one structural feature of considerable importance concerning which we have insufficient information. That is the location of the anal opening. According to all writers except Haeckel (1896) this opening is adoral in position. Haeckel in *Placocystis* locates it on the ventral surface of the animal at the junction of the column with the theca. As a matter of fact, considering the high degree of specialization to be found in this group, one would naturally expect an adcolumnal location for the opening, which would only be consistent with modifications to be observed in the case of other prostrate, actively moving Cystidea. If the anal opening in *Trochocystis* actually be adoral, then I feel that we may well postulate the same position for it in the case of the later forms, however. It is quite inconceivable that between *Trochocystis* and *Mitrocystis* this opening should have shifted from the distal portion of the theca to its extreme proximal extremity.

General discussion of the Cystidea of Group I.—Consideration of the facts as here presented in regard to the stalked Cystidea indicates that an eleutherozoic habit was maintained among these forms from the earliest times down to their latest appearance. Indeed, it will be noted that the last cystid of which we have a record, *Anomalocystis disparilis*, of the Middle Devonian, is the most highly specialized of all the eleutherozoic Cystidea. The list of genera given above might be increased appreciably. A sufficient number of forms have been cited, however, to indicate the widespread acquisition of this form of life among the most diverse groups of the Cystidea. We know, indeed, that a few stalked cystids, particularly in the Silurian and Devonian, were permanently affixed by cementation of the distal portion of their columns. The majority of the cystids, I think we may be safe in assuming, were detached at least for the greater part of their existence, however.

This almost universal freedom among the cystids is of particular interest as apparently in no wise impairing the acquisition of symmetry and structures supposed to characterize a statozoic existence. The reason for this is no doubt that in most cases freedom among these forms merely represents non-attachment. For the greater part of their lives the animals, though free, were but slightly less sessile than cemented or rooted forms. The obvious advantages and, indeed, the necessity for postlarval free stages and their bearing on the ecology of the organisms is much the same as that among the Crinoidea. A discussion of this phase of the question is given in the case of crinoids, and most of the statements there made are equally applicable to the present types.

BLASTOIDEA OF GROUP I.

In the case of the Blastoidea, evidence relative to the maintenance of an eleutherozoic habit by the stalked forms is quite limited owing to the fact that specimens with the columns preserved are seldom found. In the case of *Pentremites*, however, a considerable number of individuals are known the columns of which are essentially complete. In these specimens it is to be noted that the stems are short and in the distal portion taper rapidly, apparently coming to a point. Weak radicular cirri are present and extend for a short distance up the column. It may be held, I think, that in this genus permanent fixation by the adults did not obtain.

Whether we may extend this conclusion so as to apply to the remainder of the Blastoidea, it is impossible to say. Considering the extreme type of an eleutherozoic habit maintained by certain Blastoidea such as *Eleutherocrinus*, it would seem that there was a decided tendency among the members of this class toward the assumption of a free mode of life. This fact and the considerable acquisition of an eleutherozoic habit by the Pelmatozoa in general point strongly to the conclusion that among the Blastoidea a detached existence was largely maintained. The evidence afforded by the distribution and segregation of the Blastoidea argues quite as strongly in support of this conclusion as in the case of the Crinoidea, where this phase of the subject will be fully discussed.

CRINOIDEA OF GROUP I.

To put upon a firm footing the statement elsewhere made that the great majority of crinoid types have at one time or another, subsequent to the formation of a column, been free and capable of moving about at will, is not an easy matter. In the very nature of things the statement is incapable of absolute demonstration. The evidence in support of the contention is of two sorts. In the first place we have positive evidence as afforded by individuals in which the column is complete and shows no signs of attachment. We also have the less satisfactory evidence given by residual roots which in some instances probably indicate detachment during the life of the crinoids—whether voluntary or not we may but conjecture. On the other hand we have the more or less indirect evidence afforded by the facts of crinoid distribution and segregation. It will be unnecessary to go fully into this phase of the subject. Such facts as we have may only satisfactorily be explained, I believe, on the assumption that post-larval migration plays a part of considerable importance in the lives of the Crinoidea.

The number of stalked genera referable to the Crinoidea which were and are truly eleutherozoic during the greater portion of their lives is quite large. Inasmuch as we can only certainly postulate

such a condition of life for these forms in which we have the distal portion of the stem preserved and showing no signs of permanent fixation, it is surprising that the list is as long as it is. Were complete columns more frequently found, our list would no doubt be materially increased. In addition to those forms which from having examined complete individuals we know not to have been cemented or rooted to the bottom, we may reasonably ascribe a similar existence to many more. The reasons for such reference will be given subsequently under the discussion of the various forms. Not only are many crinoids to be considered as eleutherozoic for the greater portion of their lives, but also a far greater number are to be considered as having occasional periods of freedom during which migration is possible. In this category are probably to be placed the majority of Crinoidea.

General classification of the Crinoidea of Group I.—For convenience of reference we may divide the detached stalked Crinoidea into two groups and later subdivide these. On the one hand we have those crinoids that for the greater part of their lives are not attached to the bottom by a root or by cementation. These forms may be capable of voluntary locomotion at will, without an attendant disruption of the column. On the other hand we have those crinoids that are normally firmly affixed to the bottom, which at irregular intervals, governed no doubt by external conditions, break or are broken loose from their basal attachment and in some cases swim about freely. It is obvious that these two divisions are arbitrary at best, and differ in degree rather than in kind. In one case after a period of attachment the crinoid becomes free and thereafter remains so, barring accidental fixation. In the other case the crinoid has alternating periods of freedom and fixation. It is probable that in both divisions detachment becomes irregularly effective in different individuals, dependent no doubt on the conditions under which the particular form lives.

The crinoids that are free for the greater part of their existence may be divided according to their mode of life. Most of the types may be considered as vagile or vagrant benthos. Some undoubtedly were epi-plankton, while at least one genus may well be classed as a true plankton. In the latter cases perhaps the first step in the evolution of the forms away from the sessile stock was the assumption of a type of existence approximating to that of a vagile benthos. Gradually the exigencies of this life may be seen to have induced modifications of structure either tending toward greater freedom of movement or toward a better control of movement. As by far the most striking example of the first type of modification we may take *Scyphocrinus*, hereafter discussed, the float of which has been variously described as *Camarocrinus* and *Lobolithus*, not to mention its reference to the Echinoidea. As an example of the second sort,

the whorls of cirri of the Pentacrinidæ and other forms may be cited. The attachment of certain Crinoidea to floating bodies by which they are carried from place to place might perhaps be expected of the very young stages, but that this epi-planktonic existence should largely be assumed by certain adult forms, as we know it to be, is surprising, to say the least.

The vagile benthos.—In discussing the group of vagile benthos it may be well to deal first with those forms which from structural evidence we know to have passed a very considerable portion of their lives as detached organisms. This evidence consists either of the possession of specialized organs adapted to the maintenance of an eleutherozoic existence or a lack of special organs fitted for the permanent attachment of the crinoid.

Although permanent fixation does not become effective among these types, it is obvious that the ability to attach themselves temporarily would be of considerable advantage to the crinoids. Even among those forms referred to Group II active swimming periods are apparently of irregular occurrence and of but brief duration. Having located in some favorable spot, the crinoid needs a slight anchorage to maintain its position, as it tends to be changed by current or wave action. To meet such conditions we find various modifications, and a rough grouping may be made on the basis of similarity of such structures.

Types of temporary fixation among the vagile benthos.—Three types of temporary attachment may be recognized. In the first place, the crinoid may hold onto the bottom by a looping of the distal portion of the column about some stationary object. Secondly, there may be no true attachment, but the presence of a distal knob or anchor may serve to ballast the crinoid and maintain it in approximately the same position. Finally, as is the case more commonly among the Mesozoic and later forms, we find that attachment to other objects is effected by means of prehensile cirri borne upon the column. The order here given indicates in a broad way the general degree of complexity of the types of structure involved. The second type of fixation, if such it may be called, is quite out of the regular line of evolution, and represents both simple and complex conditions. For instance, the terminal knobs elsewhere described as occurring either on *Dolatocrinus* or *Megistocrinus* columns probably represents secretion of stereom induced by and following a violent disruption of the column. On the other hand the grapnel of *Ancyrocrinus* is a highly specialized organ resulting from the modification of radicular cirri. In the treatment of these crinoids the forms will be discussed as grouped above. The order will be changed, however, the most complex types being taken first. This is done in order immediately to make available the evidence afforded by the living Crinoidea.

Isocrinus and Metacrinus.—There is much evidence available proving conclusively that among certain recent crinoids provided with a well-developed column, a free or semifree existence is largely maintained. This conclusion was perhaps first reached by Sir Wyville Thomson, and the evidence was subsequently verified and added to by Carpenter and other writers. Carpenter's (1884, p. 18) statement of the case as affecting the genus *Isocrinus* is here given. "At the same time there appears to be ample evidence that a Pentacrinite may lead the same sort of free life that a *Comatula* does, attaching itself temporarily by its cirri." Sir Wyville Thomson long ago pointed out, in the case of *Pentacrinus decorus* (1864, p. 7), "that the animal seems to have had the power of detaching itself" at any of the syzygies of the stem in the same sort of way as the arms are thrown off during life or break up after death. He described an individual in which the stem terminated below in a worn and rounded nodal joint, and he supposed it "to have finally parted from its attachment and to have led a free life." He stated some years afterwards that this was the case in all the complete specimens which he had seen, "showing that the animal must have been for long free from any attachment to the ground." He then went on to describe the same condition as it occurs in *Isocrinus wyville-thomsoni.* "All the stems of mature examples of this species end inferiorly in a nodal joint surrounded by its whorl of cirri, which curve downwards into a kind of grappling root. The lower surface of the terminal joint is in all smoothed and rounded, evidently by absorption, showing that the animal had for long been free. I have no doubt whatever that this character is constant in the present species, and that the animal lives loosely rooted in the soft mud, and can change its place at pleasure by swimming with its pinnated arms; that it is, in fact, intermediate in this respect between the free genus *Antedon* and the permanently fixed Crinoids." The recent species to which a semifree existence has specifically been ascribed by Carpenter (1884, p. 19) other than the ones already noted are: *Isocrinus parrae* (*maclearanus*), *I. alternicirrus,* and *Metacrinus angulatus.*

The phenomena associated with the assumption of an eleutherozoic habit by the recent forms are of very considerable interest, and are of great value because of the perfect preservation of the material. Being fairly certain as to the conditions under which such types have acquired freedom, and knowing to a certain extent the habits of the crinoids, one may draw certain general conclusions relative to the fossil forms in regard to which we are not so well informed.

Method of detachment among the Pentacrinidæ.—The disruption of the column immediately distad to a nodal, and the subsequent secondary deposition of stereom on the exposed face, as shown in

Isocrinus wyville-thomsoni (Pl. 5, fig. 13), seem to be more or less characteristic of the Pentacrinidæ as a whole. In some cases it is to be noted that the deposit of stereom smoothly rounds off the entire exposed face of the distal ossicle and forms an appreciable knob. In other specimens a small plug is formed which merely closes the axial canal. In these individuals the radial striæ are at times still to be seen. It may be that these differences in the structure represent stages in the attainment of freedom, or it may be that in different species there is a certain degree of variation in this regard. The essential feature after all is the plugging of the axial canal. Subsequent deposition of calcareous matter seems merely somewhat to protect the distal nodal from fracture.

The method of detachment as it obtained among these forms is open to some question. Thomson (1869–72, p. 768) says: "There can be no doubt that in early life the Crinoid is attached and that it becomes disengaged by the withering of the lower part of the stem." Carpenter (1884, p. 22) says: "The free mode of life appears to be attained in these individuals, not by actual fracture of the stem at a node so as to shorten it more or less, but by the lower and therefore older part remaining undeveloped, while new joints appear in succession above it, each growing to a larger size than those previously formed. The stem thus becomes slender and tapering and but ill adapted for attaching itself below; but its length is not diminished so much as if it were broken at a node."

These conclusions have been based upon the fact that in many specimens there is a decided diminution in the size of the column in its distal portion. At times this decrease seems to be effected through the gradual tapering of the stem. In other cases the column tapers somewhat distad, and then decreases abruptly in diameter from nodal to nodal. As has been pointed out by Carpenter (1884), such variation in the diameter of the stem is far from being a uniform character. It is significant that adult specimens apparently do not show this structure.

On the whole, from the evidence available one would judge that a gradual tapering of the column such as is figured by Carpenter and reproduced here (Pl. 4, fig. 2) in the case of *Isocrinus decorus* is such as is due to normal growth. In cases where the column suddenly becomes smaller distad from a given point this explanation does not seem wholly adequate. It would appear that in such a case, after the detachment of the organism, a certain portion of the column ceases to enlarge.

Both Thomson and Carpenter, as quoted above, take a stand against the actual disruption of the column, but it is inconceivable that detachment could have occurred except as the result of such a process. A "withering" or nondevelopment of the distal portion of

the column would scarcely serve to separate the crinoid from its base of attachment. Whether such disruption was voluntary or performed more or less through the agency of outside forces, it is impossible to state. Involuntary detachment in the majority of cases seems the more reasonable hypothesis, however.

Concerning the exact steps in the acquisition of a detached existence in the case of the Pentacrinidæ we can not, of course, be absolutely certain. The evidence at hand permits us to draw some rather definite conclusions in regard to the matter, however. A statement of the conditions under which it is thought freedom is acquired, and of the consequent modifications in the structure of the animal, may be of value as meeting some of the objections that can be brought against the views of Thomson and Carpenter. It is possible that in different cases we have to deal with somewhat different factors—or, rather, with factors operating in variable degrees. On the whole, however, I think we are justified in assuming that the process is essentially uniform in its action.

Knowing as little as we do in regard to the embryology and very young stages of the Pentacrinidæ, we are scarcely able to form definite conclusions in regard to the nature of the immature column. The specimen of *Isocrinus decorus* (Pl. 4, fig. 2) gives us some interesting data, however. In this specimen it may be noted that the column up to within a short distance of the theca is composed of round ossicles. The proximal portion of the stem shows the characteristic pentalobate cross-section that distinguishes the adults of this type. It is probable that the distal portion of the column as shown represents the actual shape of the ossicles in the young and does not indicate a secondary deposition of stereom filling the reentrant angles of the columnals. Were the change in form brought about through such a process we would find a gradual transition instead of an abrupt change, and some of the altered columnals would be pentagonal in outline. Such, however, does not seem to be the case. The comparatively rapid change from round to pentalobate ossicles, such as may be noted in this specimen and even more clearly in a specimen of the same species figured by Carpenter (1884, Pl. 25, fig. 2), perhaps indicates a resting stage in the development of the organism after which the typical pentalobate columnals are acquired.

It is approximately at this period in the lives of the organisms that detachment occurs. As stated above, this disruption is abrupt. In all probability the point of separation comes well down in the stem. It is probable, however, that there is no definite point for the disruption of the column. Among these young specimens the length of the stem is apparently quite variable, indicating such to be the case. It is scarcely possible that in these individuals any considerable

sloughing of columnals, such as is hereafter described, could have taken place.

Subsequent to the disruption of the crinoid from its base of attachment increase in the length of the column takes place by the constant intercalation of ossicles in the proximal portion of the column. These naturally are all pentalobate in section. The first of such columnals formed agree in size with the proximal portion of the primary column, if one may so designate that portion of the stem composed of round ossicles. Subsequently, however, with the growth of the theca, there is a concomitant increase in the diameter of the columnals. This results in a marked disparity in size between the distal and proximal portions of the stem, and in periods of rapid growth, even between juxtaposed internodal series. Such a condition may well account for the structures described by Thomson and Carpenter. Such an explanation is only justified upon the assumption that there is during the period of intercalation of new columnals no considerable increase in the diameter of those already formed. I feel that we are justified in considering this to be the case.

We may well wonder in the growth of the column whether a freshly intercalated columnal, having reached the size at that time attained by the stem, is ever capable thereafter of any considerable increase in size. I doubt if such often be possible. Whenever we have an increase in the diameter of the column which is secondary its nature is immediately obvious. Usually an obliteration of sutures and an appreciable irregularity of surface mark such enlargement. In the case of adult *Isocrinus*, in the distal portion of the stem, where a secondary deposition of calcareous matter apparently occurs, the resultant columnals are no greater in diameter than the original ossicles. According to this hypothesis crinoids showing tapering columns represent normal growth without loss of distal columnals. On the other hand, forms in which the column is of practically uniform diameter indicate a considerable loss of stem ossicles. The importance of such a conclusion, were it possible definitely to establish it, is immediately obvious, inasmuch as we could then postulate a detached existence for the majority of the stalked Crinoidea.

The fact that in adult detached Pentacrinidæ we do not find any trace of this comparatively tenuous terminal portion of the column seems to indicate that it has been lost. Were it present it could only be represented as greatly enlarged by a secondary deposition of stereom. It could not be other than circular in cross section, for in old portions of the stem, even with pentalobate instead of round columnals as a base, this is the form that the ossicles tend to assume. In a few species in the distal portion of adult stems are to be found columnals that are approximately circular in outline. This form, which closely simulates that shown by the ossicles of the young

crinoid, is probably a secondary one, being caused by a deposition of calcareous matter within the reentrant angles of the columnals. In most cases the original form of the ossicles is indicated by the more or less distinct pentagonal section of the column. In many species, however, truly pentalobate columnals are to be found in the adult stages even in the most distal portion of the stem as preserved, proving conclusively that a considerable portion of the column has been lost.

If we grant the dropping off of columnals during the lives of the animals, a feature that is directly comparable to the condition found in *Millericrinus*, hereafter described, we may readily account for the structure of all the stems known to us among the Pentacrinidæ. In very young stages we should find, as we do, considerable portions of the original column of the individual. Gradually more and more of this drops off until it entirely disappears. It is probable that this dropping of columnals extends well into the pentalobate portion of the column in some species.

It is possible that the gradual loss of the distal portion of the column may be ascribed to periods of attachment followed by disruption of the crinoid from its base. In such cases detachment may occur immediately below the most distal nodal or at some higher point. The uniform termination of the columns by nodals among such types as *Endoxocrinus* suggests that detachment was had at such points. It may be, however, that the column if broken within an internode would subsequently drop off a sufficient number of ossicles so as to bring a nodal at the end of the column. The advantage of this arrangement is obvious, as the presence at the distal extremity of the column of a verticil of cirri as shown by Carpenter (1884) in *Isocrinus blakei* (Pl. 31, fig. 1), in *E. wyville-thomsoni* (Pl. 19, fig. 1), and in other species, would enable the animals readily to grasp a projection upon the bottom, and thus temporarily anchor themselves.

Factors governing length of column.—The degree to which the column is shortened probably depends to a great extent either upon the physical conditions under which the animal lives or upon the structure of the organism itself. The main factor, however, is perhaps the abundance of cirriferous nodals in a given length of column. This in turn depends upon the length of the internodals. This structural feature probably varies in different species, and may perhaps vary within any given species. A case of shortening of the internodes is shown in *Isocrinus parræ* (*maclearanus*) (Pl. 4, fig. 1). This species exhibits perhaps the highest degree of specialization known among the recent Pentacrinidæ in this regard. It will be noted in this form that each internode consists of but a single plate. Even greater compression of the nodals would give us essentially the structure to be observed in Group II. In most cases it will be observed that

forms with long internodes have comparatively longer columns than those with nodals situated more closely together. The reason for this seems to be that a certain number of cirri by which the animal is able temporarily to attach itself is essential to the welfare of the crinoid. So in cases where the internodes are long there must be a considerable length of column in order to bear an adequate number of cirri. Where a considerable compression of nodals obtains it is obvious that a much shorter column suffices.

Specialization of cirri.—The degree of specialization shown by the cirri of the recent Pentacrinidæ although not as marked as in the case of the fossil forms hereafter described, is nevertheless notable. It will be observed that the cirri are of considerable length and are equipped with terminal claws. They are quite flexible and motion is readily had in a vertical direction. The junction of the cirrus with the column is marked by a well developed articular face. The structure is clearly indicative of adaptation to considerable freedom of motion and the development of a fairly strong musculature. As has been observed in the case of living *Isocrinus* the cirri move with fair rapidity and are capable of grasping and holding tenaciously to extraneous objects.

Conclusions relative to the recent Pentacrinidæ.—From the evidence as given above, it may be concluded, I believe, that the majority of the recent Pentacrinidæ pass the greater part of their lives as detached organisms. It may be that in some individuals, after the initial period of attachment, the animal passes through alternating periods of freedom and fixation. In the majority of cases, however, it is probable that prolonged fixation only obtains in the case of the very young forms. Permanent attachment when had by the Pentacrinidæ seems to be entirely by cementation. Specimens brought up on cables show this type of structure.[1] It is quite conceivable that after a period of freedom the crinoid may well settle down and by such a secretion of stereom as is to be noted in all the specimens on the distal end of the column, cements itself to the bottom. While cementation is becoming effective, the animal could hold itself in place by means of its terminal cirri. These, after cementation, are lost.

Detached conditions among the fossil Pentacrinidæ.—Having found such universal freedom in the case of the living Pentacrinidæ we may well look for similar conditions of life among the related fossil types.

[1] Mr. A. H. Clark informs me that the statement relative to the cementation of *Isocrinus* to telegraph cables as reported by Agassiz and quoted by Carpenter (1884, p. 18) is erroneous. It is Mr. Clark's belief that fixation by cementation never becomes effective after the primary detachment of the organism. It may be that such is the case, but their seems to be no special reason why recementation should not occur. It is obvious that those physical conditions that bring about the detachment of a crinoid are not particularly conducive to its reattachment. They need by no means be prohibitive, however. There seems quite positive evidence in favor of the theory of alternate periods of fixation and freedom in the case of the Paleozoic Crinoidea, and if such conditions obtained here it does not seem at all improbable that we may have a similar habit expressed by the modern forms.

The evidence afforded by numerous writers points strongly to the conclusion that among these fossil forms a detached mode of life was largely maintained. Indeed in many of these early Pentacrinidæ, the degree of specialization exhibited by the organism is even greater than in the case of the recent forms.

Pentacrinus.—Perhaps the first ascription of a detached existence to a stalked crinoid may be credited to Buckland. In writing of the fossil *Pentacrinus* he says in part (1837, vol. 1, p. 436):

> The root of the Briarean Pentacrinite was probably slight, and capable of being withdrawn from its attachment. The absence of any large solid secretions, like those of the Pear Encrinite, by which this Pentacrinite could have been fixed permanently to the bottom, and the further fact of its being frequently found in contact with masses of drifted wood converted into jet, leads us to infer that the Briarean Pentacrinite was a locomotive animal, having the power of attaching itself temporarily either to extraneous floating bodies, or to rocks at the bottom of the sea, either by its side arms, or by a movable articulated small root.

Not only did Buckland consider these forms free, but as will be shown subsequently, in many cases he supposed an epi-planktonic existence to have been assumed by the crinoids.

Quenstedt and de Loriol both predicate a free existence for *Pentacrinus briareus* [1] and its allies, a conclusion in which Carpenter concurs. According to Quenstedt (1876, p. 271) he believed that they "köntenn gleichsam als eine Comatula betrachtet werden, deren Knopf zu grösserer Länge in einer Zeit heranwuchs, wo es noch keine eigentlichen Comateln gab." de Loriol (1878, p. 12) goes rather more into detail relative to the maintenance of an eleutherozoic habit by these forms. It is to be noted that he offers a rather novel suggestion relative to the method of locomotion in the case of these animals. He believes: "qu'ils avaient, à l'état adulte, une tige court, libre, et qu'à l'aide de leurs cirrhes très nombreux et très longs ils pouvaient nager facilement et se transporter, rapidément peut-être, d'un lieu à un autre; ils avaient aussi la faculté de se fixer a quelque objet, lorsqu'ils en avaient le désir, au moyen des crochets dont est munie l'extrémité de leurs cirrhes."

The column of *Pentacrinus briareus* as described by de Loriol (1884–1889, p. 385) is short and composed of columnals of uniform size. Each columnal is a nodal and bears a verticil of cirri. These cirri are long and highly specialized. On the whole this species indicates a degree of specialization in its adaptation to a detached existence scarcely approached by any recent form. A column essentially similar in structure has been described by de Loriol (1878, p. 7) in the case of *Pentacrinus dargniesi.* The stem in this species is held to be short and is thickly set with cirri which range

[1] Bather (1898) gives *Pentacrinus briareus* as a synonym of *P. fossilis* of Blumenbach. I here use *P. briareus* as that is the designation employed by the various authors cited. I, however, feel in no wise competent to pass on the validity of the name.

up to 100 mm. in length, each columnal bearing a verticil. Although a careful examination was made, no signs of attachment were shown by the individuals. It would seem on the evidence of these writers that *P. briareus* and its allies have essentially the same column structure, and that we may well postulate a similar habit for such forms.

Structure of Pentacrinus cirri.—The cirri in the case of these types show special and peculiar modifications that are well worthy of more than casual notice. For instance the cirri of *Pentacrinus,* as shown by *P. collenoti,* indicate a degree of specialization scarcely attained by any other stalked genus. Figures of the cirri of this species as given by de Loriol are here copied and given on Plate 5, figures 1–3. It will be noted that a terminal claw has been developed, which in itself is clearly indicative of a part of the functions of the cirri. The shape of the constituent ossicles is of very great interest. Instead of being round, they are considerably flattened. Each ossicle at its outer margins has processes projecting backward and overlapping the next preceding ossicle. There seems also to have been a less pronounced process in the median line of each ossicle. These processes and the type of articulation indicate great flexibility in a vertical direction and slight possibilities of movement laterally.

Function of Pentacrinus cirri.—The high degree of differentiation exhibited by these cirri suggest that they may well be adapted to function otherwise than simply to grasp objects. Indeed, a cirrus which is circular or somewhat oval in section and equipped with a terminal claw, would appear to have the optimum structure for such purposes. The flattening of the cirri would be of no particular value in perfecting them as grasping organs, and the very considerable development of articular ridges and pits indicates a greater mobility than would be developed were the cirri merely prehensile organs. Bearing these facts in mind, the suggestion of de Loriol quoted above relative to the part the cirri may have taken in effecting movement does not seem wholly untenable. Considering the very considerable development of cirri on one of these forms, both as to length and number, it is conceivable that even a slow movement of the cirri would be of no little value in swimming, the action of the cirri tending to elevate the crinoid.

At first blush, it seems rather far-fetched, perhaps, to consider a cirrus in any other light than as a prehensorium. When one considers, however, that in its natural medium the crinoid is practically without weight, it will be seen that even a moderate lashing motion of the numerous long cirri would have a marked effect on the animal. From the observations made by Agassiz (1888, vol. 2, p. 120), it would appear that in the recent *Isocrinus decorus* the cirri are capable of very considerable activity, it being stated that they move more

rapidly than the arms. If actually assisting in the locomotion of the animal it is evident, as suggested above, that the cirri functioned merely in raising the animal from the bottom. Lateral motion could only be effected through the action of the arms, which, on the other hand, would have slight value in bringing about vertical movement.

Effect of detachment on habits of the Pentacrinidæ.—The life history of the Pentacrinidæ as bearing on their colonial habit may be dealt with to better advantage in a subsequent paper where the facts relating to the segregation of the Crinoidea are treated in detail. A description of the conditions under which *Isocrinus* has been dredged, as given by Agassiz (1888, vol. 2, p. 117), may well be quoted at this time, however, as perhaps indicating the general habits of the detached forms. "A similar entangling also occurred among the specimens dredged by the *Blake*, and it was often very difficult to separate specimens, the cirri of which had become attached to adjoining stems. It is possible that they live gregariously, more or less united either by the twisting of the stem or the grappling of the cirri, and be only loosely attached to the ooze in which they live, or anchored more firmly by the terminal whorl to some projecting piece of rock or gorgonia stem." Döderlein (1907, p. 30) has described similar colonies in the case of adult *Metacrinus*. In this genus a considerable length of the distal portion of the column lies horizontally upon the bottom and is inextricably entangled with the columns of other individuals, corals, and other lime-secreting organisms. His description of such a colony is here given in part:

> Da, wie es scheint, diese Crinoiden gewöhnlich in grösseren Mengen beisammen stehen, förmliche "Wälder" bildend, so ist anzunehmen, dass die horizontalen Teile ihrer Stiele über und neben einander auf dem Boden liegend, mit ihren unzähligen Ranken in einander verkrallt, ein unentwirrbares, innig zusammenhängendes Geflecht bilden, das als eine mächtige, fast unzerreissbare Masse den Untergrund eines Crinoidenwaldes bildet, aus dem sich dann die einzelnen Kelche auf mehr oder weniger langen, garaden Stielen frei erheben.

In the case of both *Isocrinus* and *Metacrinus* I hold that this mutual entangling of the organisms follows a period of complete detachment during which a certain degree of movement is possible. During this period of freedom selective migration of a more or less effective sort may take place.

In this connection may be mentioned a curious belief of the Japanese fishermen relative to the location of *Metacrinus rotundus*. As is well known a large number of the specimens of *Metacrinus rotundus* have been obtained by the Japanese fishermen, who, upon hauling in their enormous trawls, occasionally find a *Metacrinus* entangled in the hooks. In this way, also, are obtained many of the exceedingly rare sponges and other organisms of this region. I have been

informed by Doctor Yatsu, of the University of Tokio, that the fishermen in laying out their lines in a given direction seldom if ever bring up specimens of *Metacrinus*. On the other hand, lines laid out at right angles to this direction frequently bring up specimens. This fact the fisherman explains by assuming that the crinoids are aligned in long courses which are some distance apart. When the tackle is laid out parallel to these lines, few crinoids are taken, but when laid across them, the conditions are more favorable. When the great length of these set lines is considered, for I have been told that they are at times a mile or more in length, it does seem surprising that were the crinoids restricted to large roughly circular areas, lines set in one direction would not be quite as apt to entangle specimens as those set in another direction.

A semilinear arrangement of small colonies rather than an approximately radial one is perhaps not wholly in accord with current ideas relative to the distribution of the crinoids, but the facts as given by Doctor Yatsu are at least worthy of consideration. It is possible that such a linear arrangement might be voluntarily assumed as directly affecting food supply. For instance, rows of crinoids at right angles to a current would have a far better food supply than closely segregated groups of individuals. On the other hand, such a linear arrangement of the crinoids may well bear a direct relation to the bathymetric range of the animals.

Evolution of the Pentacrinidæ.—The evolution of the Pentacrinidæ may only completely be worked out with the aid of extensive collections of the fossil representatives of the family. As indicated by Bather (1900) we have in all probability to start with some such type as *Dadocrinus*. We next have *Holocrinus* where the appearance of verticils of cirri is to be noted. The next stage is one that is more distinctively like the typical members of the family, and perhaps is represented by *Balanocrinus*. From such stock at least two divergent lines may be held to have arisen. One line—that characterized by *Pentacrinus*—is comparatively short lived and terminates with the group of species characterized by *P. fossilis* (*briareus*). On the other hand, we have the line that for a considerable period was no doubt made up of forms essentially similar to *Isocrinus* in structure. From this line probably are to be derived the modern representatives of the family.

Having demonstrated the widespread occurrence of a free existence in the case of certain living Crinoidea and their comparatively recent fossil representatives, it will be interesting to note similar instances of a detached mode of life among the Paleozoic forms. Only those cases will be given at this time that are of unquestioned standing. Subsequently, in the general treatment of eleutherozoic conditions as they appear to have obtained among the paleozoic Crinoidea,

those types in which detachment is predicated on the evidence of analogous structures, or for other cause, will be discussed. As more perfect material is secured, it is probable that this list of determinable free stalked crinoids will be appreciably augmented.

Mariacrinus.—A number of observers have noted that the columns of *Mariacrinus* are frequently found coiled in their distal portion. No complete stems have hitherto been recorded, however, so it has been impossible to determine the significance of this fact. Several specimens of *Mariacrinus paucidactylus* have recently come to light, the columns of which are essentially complete. From the evidence afforded by this material certain interesting conclusions may be drawn relative to the habits of this species, and by inference, of the genus.

In these specimens, which represent fairly mature individuals, the stem is remarkably short. It tapers evenly but with moderate rapidity distad and in its extreme distal portion becomes comparatively tenuous. In each individual observed, there is a loop in the distal portion of the column that forms at least one complete revolution. There are no radicular cirri present, nor is there any evidence that such appendages ever existed. Furthermore, there are no signs of cementation by a terminal plate, though to be sure, this may have been broken off. The columns as preserved indicate a fair degree of flexibility other than is shown by the looping noted above.

There can be little doubt but that this species led a detached existence for the greater part of its life. The lack of structures adapted to function as organs of attachment, and the distal coiling of the column point strongly to this conclusion. Even were fixation had by means of a terminal plate present in life, and not preserved to us at the present time, we could scarcely account for the looping of the column. This is not a feature such as is shown by statozoic types. It is probable that *Mariacrinus paucidactylus* was able to move from place to place by means of swimming motions of its arms. When the animal wished to attach itself it could readily do so by looping the distal portion of its stem about some object on the sea bottom, or perhaps about the column of another individual. The bottom of the Helderbergian sea was in places literally covered with prostrate crinoid columns and these at times may well have served as points of anchorage.

Looping of the column seems to have been present in other species of *Mariacrinus*, and we may be fairly safe in assuming that a detached existence was largely maintained in this genus. A notable instance is that of the type specimen of *Mariacrinus warreni*, which exhibits a marked coiling of the distal portion of the stem. The presence of this character in species ranging from the Niagaran to the Helderbergian strongly suggests that we are dealing with a persistent and

widespread structural feature. Hall in the third volume of the "Paleontology of New York" describes some well-developed roots as pertaining to *Mariacrinus*. This reference has slight evidence in its favor, and such roots may well belong to quite distinct genera. It is possible, however, that fixation by roots or terminal cementation occasionally became effective, and may even have persisted the greater portion of the animal's life.

Woodocrinus.—In *Woodocrinus macrodactylus* from the Carboniferous of England we have a type that unquestionably maintained a free existence. A figure of this form is here given, plate 4, figure 3, as copied from Zittel (1896), adapted from de Koninck (1854).

It will be noted that the column is fairly stout in its proximal portion and tapers rapidly distad. It is likewise quite short. There is no evidence of attachment by cementation and there are no cirri in the distal portion of the stem. The three cirri that are shown are located well up on the column, and could scarcely have been effective for purposes of permanent fixation. The distal portion of the stem is not shown as being looped but from the manner in which the column is flexed it would appear that this portion might well have been fairly mobile, and possibly prehensile. The arms are stout, and though short, might well form effective swimming organs. The cirri in this form are of considerable interest. Though not sufficiently specialized to function to any extent as prehensible organs, they yet mark the tendency to be noted in all the detached stalked crinoids toward the acquisition of such appendages.

Glyptocrinus.—In the form described and figured by Miller (1880, p. 233, pl. 7, fig. 3 *a–c*) as *Glyptocrinus schafferi*, which is almost certainly the young of *Glyptocrinus dyeri*, we have shown a most remarkable case of temporary attachment by means of a prehensile column. This type seems further to elucidate certain structures observed in widely divergent geological periods.

In this species, as shown by figures 3*b* and 3*c*, the distal portion of the column is found spirally coiled about the stem of an adult crinoid. As described by Miller the *Glyptocrinus* stem tapers distad until it becomes remarkably tenuous. In its extreme distal portion it is stated to be so small as scarcely to be visible to the naked eye. In the specimen figured by Miller the column makes no less than seven complete turns about the supporting stem. It is obvious, as suggested by Miller, that the crinoid was a freely swimming form and attached itself by will by wrapping the prehensile distal portion of its column about some object.

Unidentifiable spirally coiled columns.—In the Hamilton, Niagaran, and at other geological horizons we are well acquainted with other similar spirally coiled columns. In such cases, however, we have no means of determining the identity of the crinoids. In many of these

instances features are to be observed not to be noted in the case of *Glyptocrinus*. Although capable of attaching and detaching themselves at will, it apparently was not unusual for the crinoid to remain in any given location for a considerable period of time. As a result it frequently happens that we find the coiled and supporting columns fused together by a secondary deposit of stereom. In such cases it is no uncommon thing to find the sutures of the attached columns completely obliterated. The supporting stem is as a rule somewhat enlarged in the region where it is inclosed. In many cases it appears that the crinoid which had coiled itself about the other column, voluntarily detached itself prior to the death of the supporting organism. In other instances the fracture of the two columns appears equally sharp and indicates a simultaneous disruption.

From the wide geological range of this structure we may hold that many crinoids, particularly in their young stages, attached themselves by wrapping the prehensile distal portion of their columns about some extraneous object, preferably other crinoid stems. In many, perhaps in most cases, there was a resultant fusion of the two stems. Still later, the crinoid became detached and perhaps led a free existence. In some instances observed the large size of the spirally wound column, and the fact that it does not become tenuous in its distal portion points to the conclusion that this mode of attachment was assumed by fairly adult individuals after a period of freedom.

Mastigocrinus.—In the case of *Mastigocrinus loreus* Bather (1892, p. 200, pl. 11, fig. 3) describes and figures a specimen in which the stem is comparatively short, and smoothly rounded off at its distal extremity. It is to be noted in this individual that barring a slight tapering in its proximal portion, the stem is of notably uniform diameter. Considering the splendid preservation of the specimen there would seem to be no explanation for this termination other than that it is a normal feature, and one acquired during the life of the organism.

Calceocrinus.—Bather (1893, p. 75) cites the case of a *Calceocrinus interpres* from the Silurian of Sweden which apparently had no permanent distal attachment. The column in this specimen is 44 mm. in length. In the distal portion of the stem the ossicles diminish gradually in diameter. The last three columnals taper off abruptly "so that the stem looks very like a common earthworm." It is evident that we have here a case of complete detachment of the organism, which is all the more remarkable when one considers the extraordinary structure of the crinoid involved. As Bather says, it is scarcely safe to assume that such detachment is normal to this genus. If it were capable of being maintained in the case of one specimen there is no good reason why it should not be assumed by other individuals, however.

Ancyrocrinus.—Under the name *Ancyrocrinus* (pl. 5, fig. 9) Hall (1862) described a curious column from the Hamilton. The distal extremity of the stem is rounded off smoothly. A short distance from the end is typically to be found a verticil consisting of four spur-like appendages. These spurs may be short and stout, as is characteristic of the Hamilton of southern Indiana, or long and slender, as is shown by the New York specimens. They are perforated through the center by a very small canal which apparently does not communicate with the exterior.

At times the spurs depart from the normal arrangement, where all are in the same plane, and are variously situated at different levels. Occasionally more than four are present. However disposed vertically, their relative peripheral arrangement is the same, the orientation conforming to that of the axial canal.. The spurs are directed upward, and when but four are present the resemblance to a grapnel is very marked. It is obvious that these spurs are modified radicular cirri, in which all traces of the original segmentation as a rule have been obliterated by a secondary deposition of stereom.

Bather (1900) refers to *Ancyrocrinus* as the anchor of *Myrtillocrinus*. This reference is quite unsupported by known facts. *Myrtillocrinus* is found in America in the Onondaga limestone where no signs of *Ancyrocrinus* have ever been seen, while in the Hamilton, where *Ancyrocrinus* is fairly abundant, no trace of *Myrtillocrinus* has yet been found. Moreover, the stem of *Ancyrocrinus* is quadrangular in cross section, while that of *Myrtillocrinus* is round. Furthermore, the size of these grapnels and that of the column is out of all proportion to that of any known *Myrtillocrinus* theca.

We may hold, I think, that this grapnel of *Ancyrocrinus* served rather as a drag and ballast than as a true anchor. In a quiet sea, the animal no doubt was steadied and maintained in a fairly stable state by the weight of the terminal organ. If affected by current or wave activity, however, the grapnel might be dragged along the bottom and aid appreciably in controlling the motion of the animal. As will be noted subsequently, it is quite conceivable that the Paleozoic stalked Crinoidea, as well as their modern representatives, often lived well within the zone of wave activity. Under such conditions the advantage of such a drag is immediately obvious.

Megistocrinus or *Dolatocrinus.*—In connection with the curious grapnel of *Ancyrocrinus* should be noted certain columns found in the Hamilton group of New York State. These columns are referable either to *Megistocrinus* or *Dolatocrinus* in all probability. In these cases, the animal seems to have been detached as the result of a violent disruption. The break took place above the radicular cirri, if such were present, for there are no signs indicative of such cirri on the columns as preserved. The size of the column and its uniform

diameter likewise indicate that the break took place well up on the stem. Subsequent to the breaking off of the column, there was a secondary deposition of stereom over the fracture. Lime continued to be deposited until a knob of very considerable size was formed at the end of the stem. Such a knob is quite irregular in shape and shows no signs of cementation to the bottom. It apparently served as a ballast or drag for some freely swimming crinoid.

Such structures recall the knobs formed at the distal extremities of the columns of *Metacrinus* and *Isocrinus*, as reported by Carpenter and noted above. In the latter cases, however, the deposits of lime are of no very great size, little more than plugging the axial canal, and smoothly rounding off the end of the column. The curious object to which Barrande (1887, Pl. 4, III, figs. 1–6) gives the name *Neocystites bohemicus* seems quite certainly to be such another distal knob formed over the fractured surface of a ruptured column. The stem is unquestionably, I believe, that of a crinoid.

Herpetocrinus.—The genus *Herpetocrinus* is here held as a detached form on the authority of Bather (1893 and 1900). In this genus the column, which is a most remarkably modified organ, is coiled about the body of the crinoid, the coiling taking place in a single plane. Along a very considerable portion of the stem there are borne two rows of cirri, which are given off toward the inner portion of the coil. In *Herpetocrinus* as found, the crown lies entirely concealed between these rows of cirri.

It is evident under normal living conditions that the crinoids did not maintain this close coiling of the column, which was probably only assumed in case of irritation. It is likewise obvious that the plane of coiling could scarcely be that of the sea bottom. We must then assume when the animal was temporarily attached that it grasped some object with the cirri of the distal portion of the column, an erect position being maintained. At special times the animal could retract and assume a closely coiled position. The advantages of this coiling are not on the whole immediately obvious. A somewhat similar structure is to be observed among the Camerata, in the case of *Camptocrinus*, so the modification appears to have some good reason for its existence, divergent from the normal tendency though it be. It can scarcely be considered as purely protective, for why should one genus acquire such highly specialized protective structures when the associated organisms apparently have no need for anything of the sort, and when the physical conditions of environment appear to be quite normal?

It seems probable during the greater portion of the life of this form that a detached existence was maintained, and that attachment when effective was but temporary, and brought about through the clasping action of the cirri. It is interesting in this connection to

note that some of the cirri in the distal portion of the column are longer than the remainder, indicating that they were specially modified as grasping organs. The comparatively minute size of the crown and the extraordinary development of cirri suggest that the activity of the latter organs may have been of no small service in the propulsion of the animal. Bather (1893) has suggested that the alternate spring-like action of coiling and uncoiling on the part of the stem may have brought about movement.

Brachiocrinus.—*Brachiocrinus*, of which probably only portions of the column are known, undoubtedly was not permanently affixed. I have examined the distal portions of several *Brachiocrinus* columns and in each instance have found the same fused into a small knob (Pl. 5, fig. 8) and showing no signs of cementation.

Brachiocrinus is structurally similar to *Herpetocrinus* in that the column bears two rows of cirri. These are much heavier than in the case of *Herpetocrinus* and are composed of bead-like ossicles. The column is round, and it does not seem wholly certain that any but the distal portion bears lateral appendages. In one or two instances the portion of the column preserved appears involute. This coiling suggests, however, that the *distal* portion of the column forms the center of the coil, and not the proximal end, with the attached crown. If such be the case, we must consider *Brachiocrinus* as having the distal portion of the column flexible, more or less prehensile, and occasionally involute. For a short distance up the column is a double row of cirri, by means of which objects could be grasped. So considered *Brachiocrinus* is not closely comparable to *Herpetocrinus*, as has hitherto been thought.

Millericrinus prattii.—In the case of *Millericrinus prattii*, from the Jurassic, we have one of the most remarkable manifestations of an eleutherozoic habit to be noted among the stalked Pelmatozoa. Indeed, according to the classification here employed, it is a matter of no little uncertainty as whether to place *Millericrinus prattii* in this or the succeeding group. Dependent upon the variable degree of specialization shown by certain individuals, the species might indifferently be placed in either division. In all the preceding types we may note that the column is persistently present. It is moreover functional to a certain degree, acting as a ballast, drag, or organ of attachment for the organism. In this species, however, there is a strong tendency toward the complete elimination of the column. This form has been excellently figured and described by Carpenter (1882). Several of his figures are reproduced here on Plate 6. The characters shown by this species are apparently distinctive and not common to any other member of the genus.

The column is round and tapers quite rapidly distad. The longest stem noted is a trifle more than 50 mm. in length in the case of the

English specimens. In a specimen from France referred to this species Carpenter gives the column a length of somewhat more than 60 mm. In any case the column at its maximum is remarkably short and probably scarcely exceeds the length of the crown. In the majority of figures given by Carpenter there is no sign of basal attachment. In the case of one column, however (1882, Pl. 1, fig. 5), there seems to have been cementation or possibly attachment by lateral root-like processes. It is probable that in all cases observed other than this the animals were detached. In one specimen figured by Carpenter there is a slight flexure of the distal end of the column suggesting that this portion was prehensile and possibly employed for looping about some object as in forms elsewhere noted. The column in this individual is comparatively small. The most striking feature in connection with the stems of this species is their extremely variable length. This varies from a column having about 70 ossicles to one consisting of but a single columnal. Various intermediate stages are represented. From the facts as we have them it seems probable that the shortening of the column as shown in these forms is due to the dropping off of some of the distal columnals accompanied by more or less resorption. It does not necessarily follow, however, that this resorption is as a rule other than purely local in its action and is effective merely in rounding off the terminal ossicles. When the stump of the column is unusually short, resorption seems to affect all the ossicles to the extent of forming them into a subconical knob (Pl. 6, fig. 1). The probable steps in the process by which this shortening of the column is brought about will be given later.

The process by which freedom was attained by *Millericrinus prattii,* and the changes through which the animals subsequently passed as regards the structure of the column, hold no small interest for us, for in this process we probably see outlined the phylogenic history of the assumption of an eleutherozoic habit by the Comatulæ. Indeed, were *Millericrinus* to have possessed cirri, there is small doubt but that this very species would have formed the radicle of a line essentially comatulid in habit, and perhaps of considerable vigor. Detachment from the cemented base probably did not take place very early in the life of *Millericrinus prattii:* perhaps at a not much younger stage than is figured by Carpenter (1882, Pl. 1, figs. 6 and 8). It should be noted, by the way, that in the case of all the fairly long columns figured by Carpenter the stems are transversely fractured other than at the distal extremity, and the parts somewhat thrown out of line. This separation of the column comes at various altitudes, in one instance (1882, Pl. 1, fig. 8) being quite near the crown. It is evident that the union between the columnals is not a strong one at best. Furthermore, disruption may apparently take place at

any point; not being confined to a syzygy as in the case of the Pentacrinidæ.

Perhaps the most important question relative to the shortening of the column is as to whether the extremely abbreviated stems, as shown in figures 1 and 3, Plate 6, were produced directly by the detachment of practically the entire column, or whether the stem was shortened by degrees. Doubtless the primary disruption frequently took place well up in the proximal portion of the column, but in some cases where it did not we may well conceive of secondary shortening having occurred. In a highly specialized type we might well look for the fracture consistently to occur in the immediate proximal portion of the column. In this species, however, we should expect the location of the line of separation to be largely fortuitous. So far as our knowledge of the species goes, it appears in a general way that the older the specimen the shorter the stem. This would surely indicate a shortening of the column subsequent to the primary detachment of the organism, if found to be constantly true.

If the abbreviation of the column has been brought about by more than one disruption, such action should take place in one of two ways. In the first place we could have a shortening through the alternate fixation and detachment of the organism. The other method would be simply the dropping off of some of the distal columnals. A shortening of the column by the first method seems to be shown by the specimen previously referred to as being the only one in which attachment has been found. The column in this individual is of considerable size and would seem to indicate reattachment subsequent to a period of freedom; this in turn being followed by the detachment of the organism. Again, Carpenter says in regard to the distal portions of some of the columns that the sutures are somewhat obscured and smoothed over. This indicates perhaps not so much resorption as proximity to a point of attachment. The gradual loss of the major portion of the column by the successive shedding of columnals is quite within the bounds of possibility and would unfortunately leave no distinguishing marks. One may not conceive, however, of this process taking place by gradual resorption and the loss of one or two columnals at a time. The specimens indicate an abrupt separation of the column, resorption playing a purely secondary and minor part.

A very interesting result of this more or less complete elimination of the column is the formation of a type closely comparable to the members of Group II. On Plate 6, figure 4, may be seen a form in which but a single partially resorbed ossicle remains attached to the proximal columnal. In figure 6 this process has been carried still further, resulting in the complete loss of the column with the exception of the proximale. It is to be noted that all traces of the axial

canal and surface features of the inferior face of this ossicle, such as are shown in figure 5, have been filled and smoothed over by a secondary deposit of calcareous matter. The modified channel as thus formed simulates a centrale to a remarkable degree. It may not be styled a centrale, however, for it is a modified columnal, which a centrale is not, as will subsequently be shown. The proximale of *Millericrinus* and such stumps of columns as are illustrated by figures 1 and 3 are directly comparable with the centrodorsal of the comatulids, however, and are the result of practically an identical process working on columns of different yet not greatly unrelated types. The differences in the two cases are simply those of degree of specialization of the columns involved.

The whole tendency to be noted within this species seems to be toward the elimination of the column. It is of very great interest, then, to observe in practically all of the specimens figures by Carpenter that even in the shortened column there is a distinct countertendency toward a lengthening of the stem by the intercalation of new columnals. In some of the specimens this addition of new ossicles is quite marked, as in figure 1, Plate 1, of Carpenter's paper. Relative to the intercalation of new ossicles in the stem, there are features of no small interest to be noted in connection with the structure of the proximal columnal.

Structure of the "proximale" in Millericrinus.—Wachsmuth and Springer (1897) and Bather (1900) have placed the Apiocrinidæ in the Flexibilia Pinnata, doubtless on the supposition that there is a proximale. According to the figures of Carpenter (1882), it does not seem that there is such a persistent columnal in *Millericrinus prattii*. On the contrary, it would appear, as Carpenter himself notes, that there frequently is to be observed the formation of a new ossicle between the basals and what was formerly the proximal columnal. Figures 11, 20*b*, and 17, as given by Carpenter, may well indicate the successive stages by which the external appearance of such a columnal is marked. At first between and beneath the basals appear small subtriangular plate-like patches. These, as Carpenter says, are certainly not infrabasals. In figure 20*b*, as shown in the right-hand portion of the figure, it would appear that the radial patches had run together beneath the basals in certain portions of the periphery. In figure 17 there seems to be a continuous plate formed. In this figure it is interesting to note that those portions of the plate lying between the basals are of considerably greater height than the intermediate connecting portions lying directly beneath them. This clearly indicates the formation of the columnal by such a series of stages as has been outlined. It would appear, then, that at least during certain stages of the growth of *Millericrinus prattii* new columnals were formed immediately beneath the basals.

Possible appearance of infrabasals externally in Millericrinus and Apiocrinus.—A very interesting feature is shown by certain of these specimens, as, for example, figures 1, 3, and 4, in the appearance within the cup of certain apparently incongruous plates. Similar plates are to be noted in *Apiocrinus*, as shown in figures 7 and 8, which are copied from de Loriol. These represent *A. elegans* and *A. roissyanus*. The presence of such plates has been noted from the earliest times and by a considerable number of writers. No one apparently has endeavored to account for them except as being abnormalities. Carpenter (1882, p. 35) says:

> I can form no idea as to the meaning of these accessory plates; they are evidently without any morphological importance, or they would be more constant in their occurrence.

As here held, these plates have a definite morphic significance. In brief, I consider them to be infrabasals. The curious occurrence of these plates is due to the structure of the base. It will be noted in figure 12 as given by Carpenter, or in any figures of the proximal columnal of *Apiocrinus* figured by various authors, that this ossicle extends far up within the cavity formed by the basals. The infrabasals where observed lie, as they necessarily should, at the extreme apex of this subpyramidal plate. This gives them a horizontal position of approximately that of the top of the basals, or even higher. It may readily be seen if for any reason these infrabasals should become hypertrophied and extend outward to the surface of the theca that they would appear either between the basals or at the juncture of the basals and radials. The extension of these plates downward so as to come in contact with the proximal columnal in an external view may perhaps be considered a secondary feature. However, this condition might be reversed were the infrabasals to extend outward at a much earlier stage in the ontogeny of the crinoid. This may account for the conditions as we find them in *Apiocrinus roissyanus* (Pl. 6, fig. 7), although one hesitates to deny that the structure here observed may represent the formation of a new proximal columnal, after the manner of *Millericrinus prattii*.

This hypothesis relative to the identity of these plates with the infrabasals is not perhaps capable of demonstration without the careful dissection of a theca showing such structures. It is, however, inconceivable that the plates can represent anything else. The reason for such an appearance of the infrabasals is not obvious. The sporadic appearance of entirely new plates is even more inexplicable, however. It must be borne in mind that the forms which show such plates are near the ends of their respective lines, and it is among such types that unusual structural features are apt to appear.

The relationships of Millericrinus.—The relationships of *Millericrinus* have received but scant attention, particularly as regards the

antecedent types. As noted above, because of the supposed possession of a persistent proximal columnal the genus has been placed within the Flexibilia. The validity of the grouping upon which the order Flexibilia rests will be discussed more at length during a consideration of the affinities of the members of Group II. In this connection will be given a more detailed discussion of the homologies of the proximale and its value in classification. As has been described above, there seems every reason to believe that in the case of *Millericrinus* there is no justification of this reference, inasmuch as new columnals seem to be formed immediately beneath the basals. The structure of *Millericrinus* seems to point strongly to a derivation not far out of the line from which the Pentacrinidæ were evolved. In any case I can see but slight reason for removing the Apiocrinidæ from the Inadunata. One of the main difficulties in the discussion of the genus is the apparently heterogenous character of the forms referred to *Millericrinus* by de Loriol. It is evident that we have here included highly divergent types, and until these have been resolved into their proper groups by a careful study of the material we can get but an imperfect idea as to the status of the various types.

Epi-plankton: Pentacrinus.—Whereas the majority of the crinoids upon temporarily abandoning their sessile habits live as vagile benthos, a few assume the somewhat surprising rôle of epi-plankton. As has been noted above, Buckland (1837, p. 437), in addition to postulating a detached existence for *Pentacrinus*, assumed that in many instances the animals attached themselves to drifting bits of wood and were then carried from place to place. The arguments for such a mode of life can scarcely be better presented than in the words of Buckland himself:

> The specimen of Briarean Pentacrinite at Plate 52, figure 3, from the Lias at Lyme Regis, adheres laterally to a portion of imperfect jet, which forms part of a thin bed of lignite in the Lias marl between Lyme and Charmouth.
>
> Throughout nearly its whole extent Miss Anning has constantly observed in this lignite the following curious appearances: The lower surface *only* is covered by a stratum entirely composed of Pentacrinites, and varying from one to three inches in thickness; they lie nearly in a horizontal position, with the foot stalks uppermost, next to the lignite. The greater number of these Pentacrinites are preserved in such high perfection that they must have been buried in the clay that now invests them before decomposition of their bodies had taken place. It is not uncommon to find large slabs several feet long whose *lower* surface only presents the arms and fingers of these fossil animals, expanded like plants in a Hortus Siccus, whilst the *upper* surface exhibits only a congeries of stems in contact with the under surface of the lignite. The greater number of these stems are usually parallel to one another, as if drifted in the same direction by the current in which they last floated.
>
> The mode in which these animal remains are thus collected, immediately *beneath* the lignite and never on its *upper* surface, seems to show that the creatures had attached themselves in large groups (like modern barnacles), to the masses of floating wood, which, together with them, were suddenly buried in the mud, whose accumulation gave origin to the marl, wherein this curious compound stratum of animal and

vegetable remains is embedded. Fragments of petrified wood occur also in the Lias, having large groups of Mytili, in the position that is usually assumed by recent mytili, attached to floating wood.

I have examined similarly preserved material, and attached to one bit of wood not more than 15 inches in length by 3 inches in diameter there were to be found 20 or more *Pentacrinus*. Walther has brought forward similar evidence relative to the fossil Pentacrinidæ. It is probable in such cases that the attachment was not one of cementation. Although the nature of the association could not be accurately determined in the material examined, it seems highly probable that attachment was had by means of the radicular cirri. Walther considers the crinoids to have wound their stems about the drifting wood, as may well have been the case in some instances. As he shows, the attachment was so firm that frequently the crinoids were carried up into brackish or fresh water embayments, where they were deposited in the coal beds then forming. In such cases the driftwood with the appended crinoids may well have been driven in by storms.

It may be argued that in the cases above cited the wood to which the crinoids were attached was not floating at the surface, but had become water-logged and sunk to the bottom. Indeed, it is hard to see how the crinoids primarily became attached to the wood, providing the latter were at the time freely floating. Although one may concede considerable freedom of motion to the vagrant stalked crinoid, it does not seem probable or possible that the forms could swim freely at the surface. The mero-planktonic larvæ apparently offer the most feasible solution of the problem, but here another factor must be considered, and that is the length of time wood will float. Obviously in the present instance the period would have to be of sufficient length to permit of the maturation of the crinoid from an early larval stage. The arguments presented by Buckland and quoted above seem fairly conclusive that the wood with its pendant crinoids did float at the surface. The evidence brought forward by Walther likewise tends to prove that the crinoids were true epi-plankton. Were this not the case, it would obviously be impossible for the crinoids to have been driven into the brackish-water deposits where they were found. If this be true, it seems probable that the animals had passed the greater portion of their lives so attached.

Plankton: Scyphocrinus.—Unquestionably the widest deviation from the normal habit of the stalked Crinoidea is to be found in the case of the genus *Scyphocrinus*. For a crinoid to assume the rôle of a vagile benthos is not remarkable, and indeed one is not surprised to find an epi-planktonic existence sporadically maintained, as in the case of *Pentacrinus*. To find a stalked crinoid acquiring such structures as enable it to maintain a truly planktonic existence, however, is a most anomalous condition of affairs. Nevertheless, such we find to be the case in *Scyphocrinus*.

The question as to the relationship of *Scyphocrinus* to the curious bodies described as *Camarocrinus* by Hall and *Lobolithus* by Barrande has never satisfactorily been decided. The latest author (Schuchert, 1904) to deal with the subject leaves the matter open for further evidence. He, however, inclines to the belief that "*Camarocrinus*" is the distal expansion of a crinoid stem. This crinoid, in his opinion, may or may not be *Scyphocrinus*. I have recently determined *Scyphocrinus* from the "*Camarocrinus*" beds of Oklahoma, western Tennessee, and West Virginia. The material is in an excellent state of preservation and there is no question as to its generic affinities. The specimens are closely associated with "*Camarocrinus*," in some cases the crinoid lying in contact with fragments of the bulb. The finding of *Scyphocrinus* associated with "*Camarocrinus*" in such widely separated regions as Bohemia, Tennessee, Oklahoma, and West Virginia is practically proof positive that the bulb "*Camarocrinus*" is a part of the crinoid *Scyphocrinus*. Of the fact that "*Camarocrinus*" forms the distal extremity of a crinoid stem there can be no question.

Schuchert (1904, p. 268) points out that the one "weak point in the argument that *Camarocrinus* is the float or specialized root of a crinoid" lies in the fact that there are no beds bearing quantities of *Scyphocrinus* crowns to correspond with those beds bearing vast numbers of *Camarocrinus*. The reason is obvious. Let it be assumed that *Scyphocrinus* was a floating organism, and pelagic in habitat. Upon the death of the animal, as is well argued by Schuchert, the crown and stem would drop off, leaving the bulb free. The point is that the decay of the tissues would probably result first in the disintegration of the arms, next the disarticulation of the constituent elements of the theca, and finally in the breaking up of the stem. The result of such a process would be the widespread dissemination of crown and stem fragments. Under exceptional conditions the theca might separate from the stem while still intact and be so preserved. Again, the segregation of bulbs indicates that they were pocketed, as it were, in an area of comparatively quiet water after having been transported by current or wind action. The animals themselves might well have been pelagic organisms, living far out in areas still covered by the ocean. If so, the crown and stem might have been lost in most cases before coming within the range of known deposits.

Both Jahn and Jaekel (in Schuchert, 1904, p. 259) consider it probable that the bulbs may belong to different genera of crinoids. Schuchert favors this view also. Jaekel's point of view may be summed up in his own words:

> I am still the more convinced that they are bladder-like developments of roots. These at all times had an indifferent character and under similar local conditions did develop similar forms at very diverse places in the Pelmatazoa.

Apparently the main objection to referring all the "*Camarocrinus*" to *Scyphocrinus* lies in the vertical range of the forms. Putting aside the Bohemian beds, the correlation of which, with American formations, can be but approximate at best, we have "*Camarocrinus*" ranging from the late Manlius into what is correlated with the lower New Scotland.[1] This is certainly not an excessive vertical range for a crinoid genus. On the other hand, the possibility of the acquisition of such a highly specialized organ, which is without a close parallel in all the Pelmatozoa, as a result of parallelism or convergence, is beyond the bounds of legitimate speculation. It is probable that during the long period of time in which this highly specialized float was being evolved sufficient changes may have taken place in the crown to warrant generic separations. Among the forms as we know them, however, the float has essentially the same structure, and it seems probable that the animals themselves did not vary greatly. Again, the Bohemian occurrence is considered the lowest, while the Tennessee-Oklahoma occurrence is at the highest known horizon in which "*Camarocrinus*" occurs. If the crinoids to which the floats belong are referable to the same genus, even though found at the extremes of the geological range of "*Camarocrinus*," there seems no way of escaping the conclusion that the intermediate forms likewise must be considered as belonging to *Scyphocrinus*. It seems as firmly established, then, as such a thing may well be, that the bodies known as *Camarocrinus* or *Lobolithus* are the distal expansions of *Scyphocrinus* stems.

Schuchert (1904) has so thoroughly described the structure of these loboliths that there is little more to be said in that regard. More recently Sardeson (1908) has written in regard to these bodies, particularly as to their evolution. An extended discussion of the subject is somewhat out of place in the present paper and will be reserved until such time as the species of *Scyphocrinus* in America, of which there are no less than four, are described.[2]

[1] Fritsch (1907, p. 5) has described and figured a large roughly lobate object from a quartzite of Etage D as *Camarocrinus* (*Lobolithes*) *quarzitarum*. The nodular mass is some 21 cm. in breadth by 15 cm. in length, and seems to be divided into five irregular lobes. There is apparently no good reason for considering this mass other than in the light of a quartzitic concretion. It certainly bears no relation to "*Camarocrinus*."

[2] In connection with the remarkable habits of *Scyphocrinus* should be noted an interesting feature occasionally shown by the stalked young of *Antedon bifida* (*rosacea*). Mr. A. H. Clark has called my attention to a passage by W. B. Carpenter (1866, p. 726) in which the young are described as floating at the surface in an inverted position. How this position is maintained is not stated, but it would appear that the expanded basal disk has much to do with the matter. It even seems possible that cavities within the disk may convert this organ into a sort of float not greatly dissimilar to that of *Scyphocrinus*.

In *Antedon* the acquisition of such structures may be pathologic, but the case nevertheless suggests many interesting possibilities. For instance, it may well be that the float of *Scyphocrinus* had its inception in such an aberrant saltation, being first acquired in a rudimentary way by the very young crinoids. Again, it does not seem impossible that such floating disks may largely have been possessed by various crinoid lines as normal structural features. If this be true it is evident that we have a factor that might be of high importance as affecting the distribution of the Crinoidea.

Crinoidea probably referable to Group I.—In the foregoing discussion of the eleutherozoic stalked crinoids only those forms have been cited regarding which there can be no question as to the validity of the asseveration. There are a number of genera, however, which we may hold to have largely maintained a detached existence with almost as much reason as in the forms described. Still it is only because of the known association of a detached existence with certain structural features that we may reasonably predicate a similar mode of life in the case of the following genera. It will be noted in these various types that we have structures analogous to those that obtain in many of the eleutherozoic crinoids hitherto described.

Porocrinus.—*Porocrinus* is perhaps the most primitive type to be considered in this collection. The notable breadth of the column in its proximal portion and the marked rapidity with which it tapers distad, together with the comparative tenuity of its distal portion, strongly indicates that we have here a column comparable to that possessed by many of the detached cystids. In all probability we may consider that the members of this genus led the existence of vagile benthos and attached themselves at will by wrapping the distal portion of the stem about some object.

The Rhodocrinidæ.—In the case of the Rhodocrinidæ we find at least three genera in which we may well consider a detached existence is largely maintained. In *Rhodocrinus* itself, as shown by the Kinderhook species where the columns are well preserved, the stem is comparatively short and we may note a marked tendency toward looping in its distal portion. In *Acanthocrinus rex*, as figured by Jaekel (1895) we find the distal portion of the column coiled, which is evidence that the stem was not firmly affixed to the bottom. It does not seem improbable that the crinoid may well have been temporarily attached by wrapping its column about some object. From the size of the stem in this specimen one would scarcely think of it as being prehensile, however. Jaekel lays considerable stress on this coiling of the column, and uses it as one of the characters to differentiate the genus from *Rhodocrinus*. As noted above, the feature is probably quite as characteristic of *Rhodocrinus*. In *Diamenocrinus jouani* as figured by Oehlert (1891) the distal portion of the column is represented as closely rolled into a coil consisting of at least three volutions. This coil is in a single plane. As in the case of *Acanthocrinus*, the column is of large size, and from the tightness of the coil one might conceive that its function was rather in the nature of a ballast or drag than a means of temporary attachment by looping about some object. The same explanation may well apply to *Acanthocrinus*. From the remarkable similarity which we observe in these three rather divergent genera as regards the coiling of the

distal portion of the column I think we may well assume that a detached existence was largely maintained within this family.

Homocrinus scoparius.—In *Homocrinus scoparius* cirri are borne for a considerable distance along the distal portion of the column. These cirri are short and feeble, and both because of their extent and their structure may not be held as roots. In well preserved specimens it will be noted that the extreme distal portion of the column is coiled into several volutions. Such a stem is figured by Talbot. (1905, pl. 3, fig. 3.) It seems highly probable from the structure of stem in this species that a detached existence was maintained. In an earlier species of the genus the distal coiling is perhaps even more marked, but there is no sign of the presence of radicular cirri.

Camptocrinus.—In *Camptocrinus*, which simulates to a remarkable degree the column structure of *Herpetocrinus* heretofore described, we may perhaps predicate a detached existence on the basis of this similarity alone. Furthermore, a careful examination of a large number of well preserved individuals of the genus has failed to show any signs of permanent distal fixation. The functions of the cirri in this genus may be held as similar to those of *Herpetocrinus*.

The Platycrinidæ.—Among the Platycrinidæ there is a certain compact assemblage of types marked by such forms as *Hapalocrinus* and *Cordylocrinus* in which the presence of verticils of cirri strongly point to the conclusion that these forms were free. I have examined hundreds of examples of *Cordylocrinus* and seldom have found the column greatly to exceed the height of the crown. There is no sign of permanent fixation. Where the preservation justifies an opinion it seems that the column ends distally with a cirriferous nodal, after the manner of the Pentacrinidæ. In *Cordylocrinus plumosus* the cirri reach an extraordinary length. In some cases those cirri borne by the proximal nodals reach beyond the tips of the arms. The presence of verticils of cirri may in any case be held as strongly indicative of the eleutherozoic habit of the animal to which they belong. Such an excessive development of these appendages points almost with certainty to this conclusion.

Evidence relative to widespread detachment among the stalked Crinoidea.—The list of stalked crinoids which probably maintained a detached existence might largely be increased. A sufficient number of cases has been adduced, however, clearly to show the prevailing tendency to be noted among the Crinoidea. Examples have been chosen from each order and from widely dissimilar families. If a detached mode of life obtains among these divergent types uniformly and not as the result of fortuitous disruption, we may well expect among other related families and genera that a similar tendency is manifest. It rarely, if ever, is found that in a relatively homogeneous group like the crinoids any decided departure from the normal

is restricted to an isolated group of organisms. Rather, such departures are found to have taken place again and again in a more or less marked manner, not only in contemporaneous, but in antecedent and subsequent forms. As regards this particular modification, or rather habit, we find evidence that indicates its appearance from the earliest times to the present, and among most diverse types.

In the case of the majority of the crinoids described above, freedom may be held to obtain during a considerable part of the lives of the animals, at least throughout the greater portion of the adult stages. Among the Crinoidea as a whole we shall consider that detachment becomes effective for variable periods, and perhaps alternates with times of fixation. This is sufficiently inclusive, I think, to cover any case. It is obvious that it is among types where detachment becomes irregularly effective that we have the progenitors of those forms which constantly assume and maintain an eleutherozoic habit. It is no doubt among these forms again that we have the ancestors of those crinoids which in the aggregate make up Group II. No line, except of the most arbitrary sort, may be drawn between the types in which detachment is the exceptional condition and those among which it is the rule. In all we observe to a greater or less extent the operation of the same tendency becoming progressively more effective.

In the following discussion evidence of detachment by the crinoids, whether structural or of whatsoever nature, is given. The matter relative to crinoid segregation and migration has a most important bearing on the question, besides indicating in part the reasons for the assumption of such a type of existence. Such evidence as is submitted is more or less general in that such facts as are adduced from specific types may be held to apply with greater or less force to the remainder of the stalked Crinoidea. In the case of the structural evidence again the material in most instances is incapable of exact identification and can only be credited in an indefinite way to the then existing crinoid fauna.

The evidence relative to these crinoids that are universally supposed to be firmly affixed from the time the column is formed and in which an eleutherozoic habit becomes but irregularly effective, is of necessity not conclusive. Such facts as are available, however, seem to make the conclusion that sporadic and perhaps long-continued periods of freedom are of comparatively common occurrence, the only feasible one. It is these post-larval periods of detachment that probably have had more to do with the segregation of the Crinoidea than the aimless wanderings of their ciliated larvæ, and it is no doubt in no small part due to the same factor that the Crinoidea owe their perpetuation as a virile stock.

In the Paleozoic rocks we have considerable evidence going to show that the Crinoidea became detached from their roots or disks of cementation at various stages in their development. In a very great number of cases it seems quite certain that these residual roots as we find them do not indicate the death and disintegration of the crinoid, but rather a separation of the crinoid from its point of attachment during the life of the individual. In some cases, at least, disruption seems to have been voluntary, resorption apparently taking place at the point of detachment.

In certain formations—the Hamilton for instance—one is accustomed to see large numbers of calcareous disks attached to brachiopods, corals, crinoid stems, and every conceivable support. Each of these disks has a stem cicatrix, and at one time obviously constituted the distal extremity of a pelmatozoan column. As a rule these basal expansions are small, ranging from 2 to 5 mm. in diameter. The stem cicatrix is seldom sharply defined, showing that there was probably a partial resorption of the stereom at the junction of the disk and column. It is evident that these disks pertain to young crinoids and are directly comparable in function to the so-called "dorso-central" of *Antedon*. It is equally evident, I think, that these young crinoids became detached and shifted to another locality where they may or may not have become permanently anchored.

An interesting locality where such basal disks are particularly plentiful is in the Trenton limestone of Kirkfield, Ontario. Here at one time the sea advanced over an eroded limestone surface. With the advancing sea, and probably in very shallow water, came in large numbers of crinoids. The old limestone bottom is covered with basal disks, as many as fifty having been counted in an area of a square foot. Most of these disks are small, but occasionally the highly specialized basal expansions of *Cleiocrinus* are found, ranging up to 5 or 6 cm. in diameter. In many cases it seems probable that the crinoids became voluntarily detached. Stems and crowns are rarely associated with these basal expansions, and frequently the zone of detachment shows signs of resorption. It may be argued that instead of being a case of resorption in these instances it is a case of partial solution of the calcareous matter subsequent to the violent disruption of the column from the base. The splendid condition of such crinoids as are found at this horizon where the most delicate ornamentation is beautifully preserved, and the unaltered sharp angles of broken columns tend to refute this argument, however. Another example of this sort is in the Silurian of Waldron, Indiana. Here in one bed are found great numbers of crinoid roots, most of them probably belonging to *Eucalyptocrinus*. Stems and crowns, again, are rarely associated with these roots. It seems probable that here

was a colony of adult *Eucalyptocrinus*, the members of which for some reason or other, became detached and left this immediate locality.

It must necessarily follow upon the death and decay of a crinoid that residual roots or basal disks are left and many roots referable to adult specimens may no doubt be assigned to this category. The vast number of immature disks which are to be found can not, I think, be explained on this basis, however. Again, in the case of detachment for this reason, there would be no sign of resorption at the line of separation, such as is indicated in many examples. This point is equally effective against the hypothesis of violent disruption in such instances as it is to be observed. Even were there no signs of resorption at the point of detachment these basal disks need by no means be considered as having been left by the death and decay of the animals. Disruption of the column may well become effective elsewhere than at its juncture with the base. Indeed from the little we know in regard to such matters it appears that the separation of the column occurs with great frequency at higher points. Subsequent to such a type of detachment, which on the whole I think we may consider, as a rule, involuntary, the residual columnals will become disarticulated and leave a base with a sharply defined stem cicatrix.

In connection with these residual disks should be recalled those spirally coiled columns noted above under the discussion of *Glyptocrinus*. In these specimens the distal portion of a stem has been spirally wound about the column of another crinoid, in many cases being laid on as neatly as thread upon a spool. Subsequently, a fusion has taken place between the two columns resulting in the absolute fixation of the attaching organism. Most of the stems attached in this manner indicate that as in the case of *Glyptocrinus*, the crinoids were comparatively young forms, and became detached later in life.

It must be granted that those forms in which the distal portions of the columns do not bear roots or disks of cementation were not firmly affixed to the bottom. Furthermore, those types having cirri obviously adapted for grasping or in which there is a very considerable development of the cirri, may be considered to have led an eleutherozoic existence. It seems possible to carry this postulate of a free existence among the stalked crinoids still further. In other words, it seems quite probable that many crinoids having rootlets were never permanently attached. This reference is made from conditions as we have them in the preservation of crinoids in the colonies of paleozoic times.

Were the crinoids to have been truly rooted, the distal portion of the stem must of necessity have been buried in the material composing the bottom. Upon the death of such forms it is obvious that without very considerable disturbance of the sediment surrounding these

roots they could not have been freed without at least destroying the comparatively delicate cirri. An examination of the crinoids composing a colony where the animals are almost perfectly preserved furnishes no indication of any considerable disturbance. The bottom upon which they lived is in apparently the same condition as it was in Paleozoic times. Notwithstanding this fact a very large number of crinoids which retain their columns have the radicular cirri preserved most perfectly, and the distal portions of the stems are essentially complete. Such conditions apparently indicate that those particular crinoids were never firmly rooted.

In the case of the Waldron bed, containing large numbers of roots probably pertaining to *Eucalyptocrinus*, it would seem that the opposite condition of affairs obtains, and that here the roots were buried in the sediment. As found to-day, such a root is practically as perfect as during the life of the animal, but, unlike the free type of radicular cirri, it is not found attached to complete columns. It is evident that such roots as those of *Eucalyptocrinus* were buried in life, and upon the disruption of the column remained behind. One complete specimen of *Eucalyptocrinus* has been found, but this is a young individual with a comparatively small root. A notable difference is to be observed in the structure of such roots as have just been mentioned and those which are found free. In the former case the roots are confined to a comparatively small portion of the distal part of the column. They are numerous and branch frequently, having much the appearance of the roots of a tree. In the latter cases the cirri are comparatively delicate, irregularly placed along the column, and few in number. It seems possible, then, when we observe columns of the latter type to predicate a semifree existence for the crinoids. The number of such forms is very considerable, and in most cases such evidence of an eleutherozoic habit is supplemented by a coiling or looping of the distal portion of the column.

Were the majority of crinoids firmly affixed in their adult stages, as has been commonly assumed, we should find a far greater number of roots obviously pertaining to mature animals. It is a fact that will at once strike anyone having to do with the Paleozoic rocks, and particularly those beds in which the Crinoidea are comparatively abundant, that large roots are of great rarity. This is the more remarkable when one considers the nature of these organs. Either as basal disks or radicular cirri they are, as a rule, stout and reenforced with a secondary deposition of stereom. Those roots composed of radicular cirri clearly indicate in the majority of instances inclusion in the substance of the sea bottom. Under these conditions, with deposition in quiet waters, there is no reason why practically all of the roots should not be preserved to us to-day. The preservation of the roots at Waldron, Ind., above described, should be the rule and not the

exception. Here the cirri are preserved even to the most tenuous extremities.

Crinoid crowns, with their comparatively weak articulations, are found in the utmost perfection. These, moreover, lay upon the sea bottom and were not already covered. Comparing the two extremities of a crinoid, all the chances for preservation lie with the roots. The relative proportions in which the two are found, however, would tend to prove quite the opposite. The crowns and calices far outnumber the roots. The only logical deduction from these facts is that there were in reality more crowns than roots—in other words, that a very great number of the Paleozoic Crinoidea, like their modern relatives, led a semifree existence. At any rate, we may assume that they had no highly specialized organs for purposes of permanent fixation.

One must constantly bear in mind that universal freedom is not predicated for any given time or for any given group. It was constantly assumed in a number of sporadic lines, but these may be held as exceptions to the general rule. In some species and genera, no doubt, an eleutherozoic existence was of very rare occurrence. Certain specialized roots bear witness to this fact by their great abundance. In the case of the easily recognized "*Aspidocrinus*," for example, which is the basal expansion of some apparently adult crinoid column, hundreds of specimens may be collected in certain beds. No crinoid crowns are found associated, having doubtless decayed and been reduced to their constituent elements. Such an instance illustrates the proper proportion one would think should obtain between crowns and roots, were there originally an equal number of each, and were the bases of attachment practically indestructible under normal conditions. The proportion should be more nearly equalized in cases where the roots are composed of cirri, perhaps, for here there is a greater chance for the roots to be destroyed.

The evidence as afforded by available facts relative to the material discussed above seems to warrant the drawing of two general conclusions. In the first place we are fairly safe in assuming a fixation of the crinoids in their early stages, which was frequently, perhaps universally, followed by a period of detachment and freedom. In the second place it seems highly probable that there was a widespread lack of fixation among the mature crinoids. Given freedom and more or less ability to move, we may easily see that the crinoids could largely determine and control their movements, and consequently their environment.

As suggested above, it seems highly probable that these periods of postlarval freedom bear largely on the distribution and segregation of the crinoid elements in the various faunas and have much to do

with the cosmopolitan nature of many forms. The facts relative to the distribution of the Crinoidea, on the other hand, offer many convincing arguments in favor of the widespread freedom of the adult crinoids. Inasmuch as these facts apply with equal force to all the Pelmatozoa discussed in the paper, it has seemed best to postpone a treatment of this phase of the subject until the different groups have been discussed in detail.

In such Crinoidea as those above noted in which a detached existence has been shown, there can be no question but that for a large part of their lives the animals were capable of more or less free movement. In the case of any given species where such freedom of movement has been established, it is not held that every individual necessarily enjoys the same freedom. In any species of *Isocrinus*, say, it may be found that there are individuals the greater part of whose lives is passed cemented or rooted to one spot, while others undoubtedly pass long periods of time during which there is no such fixation. It should be borne in mind, however, that the status of such a free type is not that of a sport, freedom being accidentally acquired and inadvertently maintained. Rather it should be held that such a type of life is, as one might say, optional with the crinoid, freedom in such instances perhaps being accidentally acquired, but in most cases being voluntarily maintained. In all such types freedom is the expression of a general tendency toward the assumption of an eleutherozoic habit and in all probability would not be perpetuated were it not for this fact.

Group II.

As previously defined, this group contains those Pelmatozoa which have lost all or the greater portion of their columns. In certain fossil forms the stem is completely eliminated, not even the proximal columnal being retained. In one very large, and perhaps the most important division of the group, however, it is next to impossible to draw a line separating the constituent members from the forms characterizing Group I. In this division, the "Comatulæ," the proximal portion of the column is retained, which is, as a rule, profusely cirriferous. It seems to be a question as to whether these genera should be placed in Group I or whether such a type as *Millericrinus prattii* should be listed under Group II. Division has here been made on the basis of the degree of specialization of the forms involved. Thus, among the Comatulæ a stem is only had in the embryonic stages and is consistently lost as a column among the adult crinoids. Among the ancestors of these forms, however, we come eventually to a type which is indifferently stalked or detached and hence in a way to be held as intermediate between Group I and Group II.

It is among the members of Group II that we find the highest expression of an eleutherozoic habit among the Pelmatozoa. This does not signify that among these forms we have the highest degree of specialization and modification, although even in these respects the crinoids are notable. We have here, however, the most perfect adaptations to a free-swimming life. Such adaptations are best shown among the Crinoidea and but imperfectly developed in the case of the Cystidea and Blastoidea. This is obviously due to the fact that among the latter classes the brachial appendages have been but indifferently developed, and are scarcely able to function as active swimming organs. Among the members of this group we have a wide range in the habits of the animals. The majority of the forms may be classed as vagile benthos, locomotion being effected either by crawling along the bottom or by more or less extensive swimming movements. From such types we pass to those in which a truly pelagic existence is maintained.

Bather's classification.—Bather (1896, p. 995) considers that unstalked crinoids "fall into three distinct groups." These are:

> First, the group in which a portion of the stem remains, becoming modified into a cirrus-bearing centro-dorsal, as in *Antedon*, *Eudiocrinus*, and *Thaumatocrinus*. These forms anchor themselves by their cirri, and though capable of crawling, climbing, and swimming, do not often exercise their faculty of locomotion. Secondly, the group in which either a portion of remaining stem, or the lower part of the cup (i. e., basals or infrabasals), becomes solidified, usually by additional deposition of stereom, into a knob, which, one may suppose, serves as ballast or as a sea-anchor; such forms are *Agassizocrinus*, *Edriocrinus*, and *Millericrinus pratti*. Both of these groups have a small calycal cavity with thick walls, and there can be little doubt but that all are attached by a stem in the earlier stages of ontogeny. The third group, comprising *Marsupites*, *Saccocoma*, and *Uintacrinus*, has no trace of a stem or of any anchoring structure, but is in all respects adapted for free locomotion; the calycal cavity is large in proportion to the thickness of the arms, and is enclosed by thin flexible walls.

Classification of Group II here employed.—For the purpose of the present paper I have thought it more expedient to use a somewhat different classification. This grouping, like the one used by Bather, is a purely physiological one—widely divergent types being placed together because of a certain unity of structure in the apical portion of the dorsal cup. The grouping likewise includes several Cystidea and Blastoidea, which as regards their mode of acquisition of an eleutherozoic habit are structurally comparable to the Crinoidea of this division.

Among the majority of the forms here described under Group II the loss of the stem is a constant character and acquired as the result of a definite evolutionary process. There are, however, several crinoids where the loss of the column, though complete, appears either to be a sporadic feature, or forced upon the animal by violent disruption of the column. These crinoids shed considerable light on

the origin of certain structures to be observed in crinoids where a loss of the stem normally obtains. Because of this fact they will be discussed in connection with Group II. As will hereafter be noted, the chief interest of these aberrant types is in connection with the origin of the centrale, characteristic of Type 2.

The genera of the first division may be grouped together according to the way in which the plates of the dorsal cup and the proximal columnals become modified as a result of the loss of their articulated stalks.

Type 1.—In this type of structure the proximale (and occasionally a few of the columnals) fuses with the infrabasals forming what is known as a centro-dorsal. This centro-dorsal is usually cirriferous throughout the free-swimming stage of the individual. In some forms however, the cirri are lost in the adult. The centro-dorsal also lodges the chambered organ. Some of the genera representing this type of structure are:

Antedon.
Actinometra.
Eudiocrinus.
Atelecrinus.
Thaumatocrinus.

Type 2.—Here we find that after the loss of the stem, which is entirely detached from the crown, there is introduced an entirely new element into the dorsal cup. To this plate we shall apply Bather's term centrale. At times, as will be explained later, the centrale may fuse with all or a part of the plates in the proximal circlet of the dorsal cup. This centrale functioned as a plug to stop up the apical opening through which communication was established between the visceral cavity and the stem lumen in the stalked condition. The genera illustrating this type of structure are:

Uintacrinus.
Marsupites.
Saccocoma.

Type 3.—In this case again, the stem is entirely lost. In the typical crinoid of this group, *Agassizocrinus*, the infrabasals, which are quite large and massive, fuse, and together with a secondary deposition of stereom, close the axial canal. Apparently no centrale is formed. Some species of *Edriocrinus* are structurally analogous to *Agassizocrinus* as regards the fusion of the proximal circlet, and the secondary deposition of stereom.

Type 4.—This group has been made for the sake of completeness, to include two Blastoids and certain Cystidea. In these forms no centrale exists nor is there a fusion of the proximal circlet, and a secondary deposition of stereom. Instead, the basals unite very closely,

leaving no opening, therefore obviating the necessity of any secondary structures.

These four types of structure will now be taken up in the order here given, and a more detailed discussion given to each group.

TYPE 1.

The Crinoidea constituting this assemblage are entirely restricted to Mesozoic and recent forms. In the present seas representatives are very numerous and have an enormous range. It seems highly probable that the Comatulæ represent a number of genetic lines, and that even some of the families as defined by Bather are polyphyletic in origin. Whether sufficient material and information will ever become available to enable one closely to discriminate between these convergent lines it is impossible to say. The component genera after all have an essential unity of structure, and have doubtless been derived from not widely divergent types. Such being the case, and inasmuch as these forms are so well and widely known, no attempt will be made to discuss any given genus in considerable detail. Certain points regarding the structure of the animals are given, however, because of the bearing they have on questions dealt with in the present paper. The probable origin and development of the centro-dorsal is treated at some length, for instance, not only because of its importance in this group, but also because of the bearing it has on larger systematic questions.

During the past two or three years the comatulid genera as recognized by Carpenter have been divided and subdivided into numerous genera, chiefly through the efforts of Austin Hobart Clark. Inasmuch as the descriptions of these genera are of a more or less preliminary nature, one may be pardoned for not making use of the new appelations. For the purposes of the present paper extreme nomenclatorial refinements are after all in no wise essential. On this account very largely, no attempt has been made to depart from the nomenclature of Carpenter, and the generic names of the free-swimming crinoids as here employed are those commonly accepted.

The structure and development of the centro-dorsal.—In the well-known *Antedon*, as well as in the other genera of this group, the central apical portion of the dorsal cup consists of a centro-dorsal. This is made up chiefly of the proximale, which either persists alone, or possibly has a limited number of columnals fused with it. To the proximale also are probably fused in all cases the infrabasals. These, because of their size, are a negligible quantity in a consideration of the general composition of the adult centro-dorsal. The centro-dorsal is cirriferous, except in the adults of certain species, where the cirri have been lost.

The development of the centro-dorsal in the case of *Antedon* has been described as follows by Carpenter (1888, p. 11):

> The centro-dorsal is at first a simple ring, in no way different from the other stem joints, but when the basals come to assume a definite shape and the calyx acquires the doubly conical form of the Cystid phase, the centro-dorsal becomes distinctly wider than the annular stem joints below it and takes on a pentagonal shape. The basals rest against the sides of the pentagon, and its angles which fit in between them are therefore radial in position. * * * At this early stage the basals are only in contact with the centro-dorsal by their lower edges, but it soon begins to increase in diameter and extends itself over the bottom of the calyx. * * * It increases at the same time in vertical depth, and the first cirri make their appearance. These are radial in position, and the portion of the centro-dorsal between every two sockets rapidly enlarges, so that it comes to project beneath each basal plate, and the angles of the centro-dorsal thus become interradial instead of radial. This change is very clearly seen in larvæ which have only one or two cirri, so that one part of the centro-dorsal shows the primitive radial symmetry and another part the acquired interradial symmetry.

In this form the proximale, without the addition of other columnals, forms the centro-dorsal.

The further growth of the centro-dorsal is described on page 12:

> I merely wish to point out that as soon as the centro-dorsal of the early larva of *Comatula* takes a definite shape its angles are distinctly radial. * * * But when the cirri appear on the centro-dorsal and the basals begin to be transformed into the rosette, the outline of the centro-dorsal changes. The basals are no longer the principal plates in the calyx, but they undergo metamorphosis into the small rosette, and the centro-dorsal increases rapidly in size, more so than any other part of the skeleton, "so that it soon comes to pass beyond the circlet of basals and to abut on the proximal edge of the first radials; and instead of stopping here it continues to increase in diameter until it conceals the whole inferior surface of the first radials and sometimes even encroaches somewhat on the second."

Carpenter, in these passages, as elsewhere, insists upon the primitive radial position of the centro-dorsal, as opposed to the views of Wachsmuth and Springer (1879–86, pt. 3, p. 298 (222)). Moreover, he proves his point conclusively by giving two figures of larval *Antedon*, one of which is reproduced here. (Pl. 7, fig. 6.) In the very early stages, and before the appearance of the cirri, the centro-dorsal conforms to the pentagonal opening formed by the basals, and hence by necessity the angles must be radial in position.

In their Monograph of the Camerata (1897, vol. 1, p. 64), Wachsmuth and Springer try to controvert the statements of Carpenter above cited. On Plate 6, figs. 18 and 19, they reproduce two figures taken from W. B. Carpenter. Discussing these figures in the text, they make the following statement:

> The centro-dorsal at the Pentacrinoid stage of the Comatulæ, as may be seen by examining Pl. 6, figs. 18 and 19, agrees closely with that of the Apiocrinidæ. It is interradially disposed at the proximal face, and also at the distal face, so that its angles correspond with the angles of the basals as in those dicyclic Crinoids whose infrabasals are hidden by the column, and even in the prefloating stage the centro-dorsal retains its interradial position.

Figure 19, according to the explanation of the plate, is an adult specimen, and figure 18 certainly does not represent a very young stage. Wachsmuth and Springer apparently overlook the fact that Carpenter described the centro-dorsal in the later stages of development as having interradial angles and conclusively proved that this was purely a result of secondary growth. Indeed, as quoted above, Carpenter states that in larvæ in which only one or two cirri have appeared, the centro-dorsal in the noncirriferous portion is radial, while in the remaining portion the angles of the plate are interradial, as a result of secondary change of form induced by the presence of the cirri.

Bather (1898, p. 425) again emphasizes this fact:

> That such secondary formation of stereom does take place is no hypothesis; it has been described in *Antedon* by W. B. Carpenter, H. Bury, and others. In fact, the odd thing about that genus is that the very features on which Wachsmuth and Springer relied in their famous prediction that it would be proved dicyclic are of purely secondary nature.

Thus we find that the early form of the centro-dorsal in *Antedon* is entirely dependent upon the nature of the adjacent basals and is largely governed in subsequent growth by the addition of cirri and the concomitant increase in size of the plate itself.

It would have proved much more effective had Wachsmuth and Springer applied their law to the primary verticil of cirri, instead of attempting to make the centro-dorsal conform to their law; for these cirri are radial in position, as they should be in a dicylic form. The later cirri are given off apparently without regard to position.

It is to be noted in the case of *Antedon* that the proximal columnal fuses with the infrabasals at an extremely early stage in the ontogeny of the animal. Indeed such fusion apparently takes place before the constituent plates of the theca have assumed definite positions and have become apposed. Such a condition of affairs shows a high degree of acceleration and clearly indicates the comparatively ancient acquisition of a detached existence by this line. As a result of this early fusion of the proximal columnal with the infrabasals the centro-dorsal assumes a position within the basal circlet as soon as the plates acquire a definite form. This condition is quite different from that to be noted in earlier and less specialized types, as will be indicated in the discussion of the phylogeny of the centro-dorsal.

In its adult expression among the Comatulæ the centro-dorsal assumes widely different forms. Primitively low and bearing but few cirri, in some forms it reaches an extraordinary development. In *Antedon* (*Solanocrinus*) *scrobiculatus* (Pl. 8, fig. 3), for example, it will be noted that the centro-dorsal is of great length. As opposed to this condition of affairs a number of species of *Actinometra* have the organ greatly reduced and noncirriferous. This type of struc-

ture has been described by various authors and some figures of *A. nobilis* are here given as copied from Carpenter. In younger specimens of this species the centro-dorsal is normally cirriferous. Subsequently, however, the cirri are lost and the centro-dorsal becomes largely resorbed (Pl. 6, figs. 9–11). Still another variant is to be observed in the case of such a form as *Antedon laticirra* (Pl. 8, figs. 1, 2). But few cirri are borne by the centro-dorsal and these are of relatively enormous size. Again, in many of the species of Comatulæ, both recent and fossil, the centro-dorsal bears large numbers of cirri either regularly or irregularly arranged. The shape of the centro-dorsal seems, therefore, to vary largely both as to shape, size, and number of cirri borne. This variation seems to obtain not only among different genera and species, but within the same species, dependent upon the degree of maturity of the individual.

Definition of the centro-dorsal.—Before discussing even in a most general way the interrelationships of the forms referred to the Comatulæ, or to endeavor to establish a connection between any of these types and their stalked ancestors it will be necessary to enter rather deeply into a discussion of the evolution of the centro-dorsal, the organ that is so characteristic of these eleutherozoic forms. It may perhaps be best to limit and define the term centro-dorsal. The centro-dorsal may be held to consist in its simplest form of the proximal columnal to which the infrabasals have been fused. Furthermore, centro-dorsal as here used may only apply to a cirriferous organ. It is evident that the terms proximale and centro-dorsal cover an essentially similar structure. Indeed, as here defined, the only essential difference lies in the fact that one bears cirri and the other does not. It is obvious that this distinction is a most arbitrary one. It is nevertheless a matter of some convenience to draw such a line. It is quite within the bounds of possibility, as will subsequently be shown, that the term "centro-dorsal" may apply to two quite different structures. As above defined and as immediately discussed hereafter, the organ is held as having the same position generally assigned to it. After having indicated in a general way the evolution of this type of centro-dorsal, the evidence for another and divergent type will be given.

Evolution of the centrale.—The question of the evolution of the centro-dorsal involves necessarily the question of the evolution of the centrale. This in turn involves questions which are quite without the province of the present paper. It is necessary, however, to state, even though briefly, an opinion relative to these topics. The presence of a persistent proximal columnal has been used by Wachsmuth and Springer and by subsequent authors as a character of prime importance in the classification of the Crinoidea. It is on this structure that the Order Flexibilia was established. I do not believe that

this structure has the importance assigned to it, but that it is a character independently acquired in several lines of evolution.

It is evident that the forms with a proximale have been derived from those having normal stem structure where new columnals are formed immediately beneath the proximal circlet of thecal plates. If this character were acquired in a single genetic line it would doubtless be of considerable value, although it would be difficult at best to distinguish between the primitive forms having such a columnal and those from which they were derived. We are dealing, however, I think, with a type of structure which may be shown to have been independently acquired by numerous offshoots from the Inadunata.

It is a question whether there consistently be such a proximale as a matter of fact. We may certainly postulate its existence in many adult crinoids, but it appears to me highly probable that in the ontogeny of many such forms we might well find fresh columnals forming immediately beneath the theca. In a number of forms referred to the Flexibilia in which the so-called proximale is notable because of its high degree of differentiation it is probable that we may frequently have the formation of new columnals proximad to this ossicle. Such, for instance, is apparently the case in the genus *Millericrinus*.

The appearance of an apparently persistent proximal columnal in *Millericrinus* is of considerable interest inasmuch as it seems to have been but imperfectly acquired within the genus. In such a form, for example, as *M. gracilis* the proximal columnal may be seen to be but slightly differentiated. In *M. prattii* as described above (p. 51) the proximal columnal, although apparently well formed, seems at times to be superseded by the formation of a new plate between it and the theca. In *Millericrinus recubariensis* as described and figured by Bather (1897), a species that Mr. A. H. Clark refers to *Bathycrinus*, the proximal columnal is said "to be incomplete; it only occupies a portion of the basal surface of the cup, and some of the basals rest, in whole or part, on the columnal next following." It will be unnecessary to enter further into a discussion of this primitive *Millericrinus*, but I think it is evident that we have here good evidence of the formation of a new columnal between the former proximal columnal and the theca. Again, within the genus we have cases in which the proximal columnal appears quite as highly differentiated as in any form to which a proximale has been ascribed.

In certain species, as in *M. charpyi* (Pl. 7, fig. 1), and less notably perhaps in *M. beaumonti* (Pl. 7, fig. 2), the proximal columnal is of great height and is considerably differentiated from the remainder of the columnals. In such cases one would not be surprised to find detachment becoming effective immediately beneath this columnal, and the crinoid assuming an eleutherozoic existence. We know that

the tendency toward this life is quite marked, as shown by the modifications of *M. prattii*.

Whether there be a truly persistent proximal columnal or not it certainly is true that in many genera at a certain stage in the growth of the organism the proximal columnal becomes differentiated in a more or less marked manner from the remaining ossicles of the column. The tendency is constantly toward a higher degree of specialization in this regard, and no doubt the structure becomes considerably affected by acceleration. A proximal columnal may only be safely called a proximale, I think, when fusion, more or less complete, has taken place between it and the infrabasals. Such a fusion alone may definitely preclude the possibility of an intercalation of columnals immediately beneath the theca. The infrabasals in any case must be small, if not practically obsolete. In consequence of this fact the proximal columnal comes to lie within the basal circlet. It is evident, however, that its contact with the circumjacent basals is not of the same nature as that of a centrale with its juxtaposed plates.

The proximale as it is shown by different genera is too well known to warrant extended description. Carpenter (1884, p. 25) describes the proximale as follows in the case of *Rhizocrinus:*

> But the uppermost joint of all is of a different character altogether. It has a pentagonal outline, and the surface, which rises gradually from the circumference toward the center by five radiating ridges into an equal number of trapezoidal fossæ that receive the lower ends of the elongated basals. Here, therefore, we find the top stem joint presenting the same character that it does in *Apiocrinus* and *Millericrinus*, and entering to some extent into the composition of the cup, while the new joints are probably intercalated below it.

Such is the essential structure of the proximale in the Bourgueticrinidæ, with which we are immediately concerned. The "proximale" as had by other families referred to the Flexibilia will not be discussed, as having but slight bearing on the origin of the centro-dorsal. It is to be noted in the description above that the proximale of *Rhizocrinus* does not present "the same character that it does in *Apiocrinus* and *Millericrinus*." In the case of *Rhizocrinus* fusion of the proximal columnal with the infrabasals has apparently become completely effective, whereas in the other two genera cited such fusion is by no means universal.

The evolution of the centro-dorsal.—Having briefly outlined the ontogenetic development of the centro-dorsal in the case of *Antedon* and discussed in a general way the structure of the proximale and centro-dorsal, we may indicate the stages by which these structures have been acquired phylogenetically. As above mentioned the generally accepted type of centro-dorsal will be dealt with first.

We must of necessity begin with a crinoid in which columnals were normally produced immediately beneath the theca. In all

probability we need not go back into the Paleozoic for such a form. Subsequently among the descendants of such a type we may postulate a tendency toward the acquisition of a proximale. The essential factor in such an evolutionary process is naturally a decrease in the formation of ossicles immediately beneath the theca and a lengthening of the stem by the intercalation of new columnals distad to the proximal columnal. It is doubtful if there are many forms among which formation of columnals immediately beneath the cup does not take place even in post-larval stages of development. The differentiation of a persistent proximal columnal may no doubt be accounted for very largely on a purely mechanical basis, though concerning its exact nature one can not be entirely certain. It is sufficient to note that at some stage in the development of the animal the topmost columnal becomes intimately associated with the proximal elements of the theca. This comes as the direct result of a gradual diminution in the size of the infrabasals. Such a tendency toward the elimination of the infrabasals brings them within and at the apex of an inverted cup in the base of the theca. This results in the introduction of the proximal columnal within the basal circlet, as regards horizontal position.

Having acquired a proximal columnal that retains its position as such for an extended period during the adult stages, there begins an appreciable differentiation of this ossicle, as separating it from the remainder of the columnals. These differences lie chiefly in a lengthening of the columnal, which may become very marked. (Pl. 7, fig. 1.) At the same time there is a more and more marked inclusion of the ossicle within the basal circlet accompanied by an increasingly close union between it and the infrabasals. Eventually in some of the later stages of development there is a complete fusion between the infrabasals and proximal columnal. At this stage we may call the columnal a "proximale" in its strictest sense.

Subsequent to the differentiation of the proximal columnal there was no doubt a constant tendency on the part of the crinoid to break loose from its column immediately beneath this ossicle. The process may in a general way be held to have evolved somewhat in the manner to be observed in the case of *Millericrinus prattii*, certain specimens of which as already described are essentially comatulid, barring the lack of specialization relative to the centro-dorsal that is to be noted in the case of the later forms. From types in which detachment occurs infrequently and perhaps at different points in the column we come to forms among which detachment becomes universally effective. Detachment at first is to be found only in adult stages, but, as affected by acceleration, was pushed farther and farther back in the ontogeny of the organisms.

The next step is marked by the acquisition of cirri borne by the proximale. This, according to definition, would constitute the formation of the first true centro-dorsal. The extreme irregularity as regards the appearance of these cirri and their variable number point to the conclusion that they are not modified verticils of cirri originally borne by a nodal. In such forms, indeed, I think we have to look among stalked Crinoidea without verticils of cirri upon the column for the ancestors of the free types. The cirri in such cases I conceive to have been evolved in direct response to the needs of an eleutherozoic habit. At the same time I do not believe that such cirri could have been evolved were it not for the fact that within this genetic line there was a tendency toward the acquisition of such organs. These cirri appearing first in the free-swimming stages perhaps are progressively found earlier and earlier in the ontogeny of the animals until, no doubt, cirri were borne at an early stalked stage in the development of the organ.

Subsequent to the acquisition of cirri the changes in the gross structure of the crinoid skeleton are of a less fundamental nature. Detachment from the column takes place at progressively earlier ontogenetic stages, as does the appearance of the cirri. There is, moreover, a constant tendency toward an increase in the number of cirri. The infrabasals continually decrease in size and importance, and a reduction in the size of the basals is to be noted. The basals, moreover, unite to form a "rosette" and do not appear externally. Naturally there are also changes in the musculature of the arms and in the type of union between the ossicles. The degree of specialization is in direct proportion to the length of time that has elapsed since the assumption of an eleutherozoic existence.

Phylogenetic steps in evolution of centro-dorsal.—The steps in the evolution of the centro-dorsal as briefly outlined above find expression in well-known fossil genera. These genera may not represent actual links in an evolutionary chain, but they have the character that such ancestral forms undoubtedly possessed. Indeed, it is by no means certain that these genera did not give rise to successful comatulid lines. If they themselves did not, forms not widely unrelated may be held to constitute the necessary ancestral types.

One may well, I think, start with such a form as the Cretaceous *Mesocrinus*, which has been described and figured by Carpenter (1881). This genus apparently has a fairly well-developed proximale, which may or may not be fused with the infrabasals. It is inserted well up in the cup formed by the basal circlet. The proximale is small, however, and bears no cirri. The columnals in the upper portion of the stem are circular in section, but the distal ossicles have oval articular faces. The column evidently pertains to the Bourgueticrinidæ. The stem in its distal portion is comparatively heavy and

bears radicular cirri. These are obviously for purposes of attachment. Apparently never more than two cirri are borne by a columnal.

In another Cretaceous genus, *Thiollericrinus* (Pl. 7, figs. 3–5), we have made a great advance. In this genus detachment had become universally effective, disruption occurring immediately beneath the proximal columnal. Even though detachment took place late in the life of the organism, as is evidenced by the large size of the articular face on the lower surface of the centro-dorsal (Pl. 7, fig. 5), the very fact of disruption being actually effective at this point, shows clearly that an eleutherozoic habit had long been maintained. This is further indicated by the presence of cirri on the centro-dorsal. As is shown by *T. herberti* (Pl. 7, fig. 3), the cirri are small, few in number, and irregularly placed. In *T. flexuosus* (fig. 4 on the same plate) the cirri are comparatively larger, more numerous, and form a practically continuous ring about the centro-dorsal. From the shape of the articular face as preserved on the centro-dorsal (Pl. 7, fig. 5) it is evident that this genus had a typical *Bourgueticrinus* column. Such a crinoid as *Thiollericrinus* might well serve as a point of inception for a comatulid line. If such be the case, it seems probable that in this particular evolutionary line none of the columnals other than the proximal one goes to form the incipient centro-dorsal. This seems to be indicated from the fact that, owing to the structural peculiarities of the stems involved, disruption constantly takes place immediately beneath the proximal columnal. From such evidence as is available, it seems possible that in many of the comatulid lines other columnals fuse with the proximale, however.

Such fusion of columnals seems clearly to be indicated in the ontogenetic development of *Antedon* as figured by Carpenter (1888, Pl. 14). Some of the figures are here reproduced (Pl. 7, figs. 6–10). These figures serve equally well to show the development of the cirri on the centro-dorsal. Figures 8 to 10 represent stages in development of a single species and as such are not subject to the structural variations that apparently obtain in the case of different species.[1]

In figure 7, the proximale is shown as the shortest columnal in the stem. There is no indication of the presence of cirri. In figure 8, the proximal columnal is still very short, but bears a verticil of incipient cirri. These are five in number and radially disposed. It is to be noted that immediately distad to the proximale there are three

[1] Mr. A. H. Clark says that these three specimens identified by Carpenter as *A. multispina* do *not* appear to belong to the same species and, indeed, may be referable to different groups. Furthermore he states that the figures are inaccurate. It scarcely seems probable that the draftsman could go far wrong in regard to the columnals, however, and the evidence of fusion having taken place, though by no means conclusive, still seems fairly good.

Mr. Clark believes that the centro-dorsal never consists of any columnals other than the proximal one. This is unquestionably true in many species, and possibly in many phyletic lines, but such inconclusive evidence as is at present available scarcely warrants a postulate of similar conditions as a universal attribute of the Comatulæ.

short columnals. The fifth columnal is much higher, and is of a rather peculiar shape. It expands from below upward, and contracts slightly in its immediate proximal portion. The shape of this columnal is unique among the other elements of the stem, and may be recognized in the succeeding two figures. Such being the case it may well serve as a datum plane for identifying the columnals.

In the stage represented by figure 9 there has apparently been a fusion of the columnals. The cirri are borne on a much longer columnal, which apparently represents the proximal columnal plus the next succeeding ossicle. This fusion can not be demonstrated, but it seems probable, inasmuch as there are but two columnals shown between the cirriferous segment and the characteristic "fifth" ossicle. This does not prove anything, for one may argue that the number of columnals between the proximale and "fifth" ossicle varies, as, for all that we know, it may. However, an extremely close union is indicated between the cirriferous segment and the next lower ossicle. As here given the suture between the two elements it drawn as well marked, whereas in Carpenter it is little more than indicated. The next lower ossicle is somewhat smaller in diameter.

In the next stage (fig. 10) there has been a complete fusion between the cirriferous element of the former figure and the next lower columnal. The "fourth" columnal has enlarged and is of practically the same diameter as the centro-dorsal above it. It would appear that a very close union exists between this ossicle and the centro-dorsal, and that the two elements are well on the way toward fusion. Upon detachment it appears that the point of disruption would logically be between the "fifth" ossicle and the practically consolidated centro-dorsal. The union between the two seems to be of a comparatively loose nature.

From the facts as shown by these specimens we may reasonably assume, I believe, that there has been a fusion of columnals with the proximale to form the centro-dorsal in this species. Indeed, I think we may be reasonably sure that three columnals in addition to the proximale go to make up the centro-dorsal. By the direct evidence as apparently afforded by a living species we may conclude then that the centro-dorsal may at times be composed of several fused columnals. The same condition seems to obtain in the case of the fossil Comatulæ, but in regard to them the evidence is even less conclusive.

Whether the fusion of several columnals to form the centro-dorsal indicates independent derivation from that had by forms in which the centro-dorsal is composed merely of the proximale such as is doubtless the case in *Thiolliericrinus*, is a question. The columnals of the stalked *Antedon*, as shown in figures 11 and 12, Plate 7, have a decidedly *Bourgueticrinus* type of structure. The evidence seems to point strongly to the conclusion, therefore, that we have to look among

the Bourgueticrinidæ for the ancestors of this genus, though not necessarily by way of either *Mesocrinus* or *Thiollericrinus*. It may well be that fusion of columnals with the proximale is a character progressively acquired in a manner comparable to that in which we note the appearance of cirri on the centro-dorsal. Fusion of additional columnals in such a case would then merely indicate a comparatively high degree of specialization.

Polyphyletic nature of the Comatulæ.—As has been elsewhere suggested, it is highly probable that the Comatulæ represent terminal members of a number of lines of development in each of which an eleutherozoic existence has been independently acquired. They may all be considered as offshoots of the same general stock, and convergence has served to evolve strikingly uniform types. Again, the different lines have had their inception at widely different time periods as is evidenced by the extremely variable degree of specialization exhibited by contemporaneous forms. It is probable that we must look among the Apiocrinidæ as defined by Bather (1900) as well as among the Bourgueticrinidæ for the ancestors of the Comatulæ. Again, it is quite within the bounds of possibility that the Pentacrinidæ may have given rise to such eleutherozoic forms.

The structural characters that seem to indicate the presence of a number of genetic lines among the Comatulæ may not here be gone into in any considerable detail. The evidence on the whole is suggestive rather than conclusive and will only become of positive value when the several lines are worked out and their mutual relationships established. The nature of the evidence is of two sorts. The first is as regards the relative specialization of contemporaneous types as indicating the relative remoteness from stalked ancestors. The second relates to the structure of the organisms, as indicating the mutual interrelationships of the forms.

The disparity in degree of specialization among the eleutherozoic forms at any given time may, if judiciously considered, be given considerable weight. Thus in the Cretaceous *Thiollericrinus* we may well have the point of inception for a comatulid line. Living at the same time were highly specialized Comatulæ, and these were preceded even as far back as early Jurassic time by equally distinctive eleutherozoic types. Concerning the high degree of development to be observed in these early fosssil forms Carpenter (1884) writes as follows:

> Besides their tendency to combine the characters of recent generic types, the Jurassic Comatulæ are remarkable for their large size, as are also the Cretaceous species. The centro-dorsal may reach from 9 to 13 mm. in diameter, which is greater than that of nearly every recent species except *Antedon eschrichti;* while this type and *Actinometra robusta* are almost the only living Comatulæ with arm-bases anything like as massive as those of the fossil species. Some of the Cretaceous forms must have been very large. Thus the united centro-dorsal and radials of *Antedon campichei* from the Neocomian of Switzerland may reach 15 mm. in height and over 20 mm. wide;

while several centro-dorsals of *Antedon* from the Upper Chalk are almost equally gigantic.

The massive arms of many of the Comatulæ seem to mark the animals as far from primitive, and certainly not as ancestral to modern types. In certain cases a biserial arrangement of the arm ossicles is had, such as for instance in *Antedon thiollieri* figured by de Loriol (1884–1889, Pl. 224). A similar form, possibly congeneric, has been described and figured by Jaekel (1891) as *Pachyantedon beyrichi*. The lack of any recorded tendency toward the acquisition of similar types of arm structure elsewhere among the Comatulæ seems to indicate that these crinoids form a distinct off-shoot from the comatulid stock, if indeed it does not indicate a separate origin for them. Bather (1900, p. 195), states that "there is also traceable in the arms a gradual attenuation * * *" when considering the evolution of the Antedonidæ. The differences to be observed are not evolutionary in the sense that there is a gradual diminution in the thickness of the arms, but rather points to a polyphyletic origin of the forms involved, or at least a considerable divergence within the stock.

Again, among most of the fossil Comatulæ as is shown by figures 3, 4, 7, 8, Plate 8, the basals are well developed and appear prominently on the exterior of the theca. Among recent forms the basals are greatly reduced (Pl. 5, figs. 10 to 12) and seldom are to be seen externally. In many cases this reduction in size may be held to be the result of a gradual evolutionary process subsequent to the assumption of an elutherozoic habit. On the other hand, as is shown by *Thiolliericrinus* (Pl. 7, figs. 3 and 4), the basals have become obsolete in the adult stages, as regards their appearance on the outer surface of the cup. This elimination became effective while the stock was yet attached or but irregularly eleutherozoic.

The axial canal traversing the central-dorsal of a comatulid is as a rule closed and smoothed over by a secondary deposit of stereom. In many cases, however, the lumen is open at the distal face of the centro-dorsal, so that its nature may be ascertained. In *Thiolliericrinus* (Pl. 7, fig. 5), the perforation is circular, or somewhat oval, corresponding to the shape of the stem-lumen in the Bourgueticrinidæ in general. In many cases, as, for instance, in certain species figured by Carpenter (1880*b* and 1881), the central perforation of the centro-dorsal is pentagonal to sharply stellate in section. How much reliance can be placed upon these features as determining independence of derivation it is hard to say on account of the insufficient data at hand. It appears, however, that they are of some value. In this connection should be noted the observation of Carpenter that the centro-dorsal of *Antedon* has a stellate lumen when the animal becomes detached from the column. This is somewhat remarkable

when one considers the *Bourgueticrinus* type of columns possessed, and the fact that the stem lumen is circular in section (Pl. 7, fig. 12).[1]

The evidence relative to the nature of the perforation of the centro-dorsal being inconclusive because of our lack of exact knowledge, it is necessary to fall back on other more obvious and satisfactory characters. On Plate 8, figure 7, is given a view of the lower surface of the theca of *Antedon depressa* from which the centro-dorsal has been removed. Figure 8 shows the normal appearance of a cup with the centro-dorsal attached. To be compared with this is the basal view of the theca of *Pentacrinus* (*Extracrinus*) *dargniesi* (Pl. 8, fig. 5). In both forms we may note a general similarity in structure, particularly as regards the development of the basals. The basals of *Antedon* in this instance, however, quite lack the petaloid markings characteristic of the *Pentacrinus* and the Pentacrinidæ in general. The specimen of *Antedon* (*Solanocrinus*) *scrobiculata* here figured (Pl. 8, fig. 4) is noteworthy in this regard. As may be seen, the articular faces of the basals have the characteristic markings of the same plates in the case of the Pentacrinidæ. Carpenter (1880*b*) has figured Comatulæ exhibiting the same type of structure. Such for instance is his *Actinometra cheltonensis* (Pl. 11, fig. 20*b*). He likewise figures a specimen of *Antedon* (*Solanocrinus*) *scrobiculata*, in which the markings are very distinct. This type of articulation may only I think be attributed to forms in which a pentalobate column is possessed at that point. The natural inference is that the stalked ancestors of such types are referable to the Pentacrinidæ, although this need not necessarily follow. It seems impossible, however, to derive these types directly from the Bourgueticrinidæ.

In connection with the statement made above relative to the possibility of *Pentacrinus* or some member of the Pentacrinidæ having formed the radical from which might have sprung a line of comatulids, should be noted certain curious structural features in the case of *Pentacrinus* (*Extracrinus*) *collenoti* as figured by de Loriol (1884–89, Pl. 199, figs. 3, 3*a*, 3*b*) showing a most remarkable modification of the normal *Pentacrinus* stem structure. In this form it is to be noted that the column in its proximal portion is of normal size, but distad it contracts rapidly forming a stump of exceeding brevity. This stem fragment consists of something like 10 columnals. In every way it reminds one of conditions as they are to be found in *Millericrinus prattii* where a few of the proximal columnals remain attached

[1] The type of column possessed by the larval comatulid is after all directly comparable to that to be found in the very young *Isocrinus*. As figured by Clark (1908, p. 88, text figs. 3 and 4), the distal portion of the column of *Isocrinus decorus* has oval columnals, essentially similar to those here figured in the case of Antedon. This fact again indicates a close relationship of the Pentacrinidæ and at least certain lines of the Comatulæ. Indeed in both types there is an essential unity of structure up to the time detachment from the larval column becomes effective. Subsequent to that time the critical difference is that the Pentacrinidæ form new columnals and maintain a column whereas the comatulids do not.

to the theca. In the present case there has probably been a disruption of the column in its proximal portion succeeded by a partial resorption of the columnals. The result of this process is the formation of a structure closely approximating to a centro-dorsal. The specimen of *P. sorlinensis*, figured by de Loriol in the same volume (Pl. 205), apparently may be explained as having the same type of structure. In this case the columnals bear numerous long cirri which had probably not yet been acquired in the specimen previously described. Such a disruption of the column in the case of *Pentacrinus*, taken in connection with what we know relative to the wide maintenance of a detached existence by these forms, indicates that there was a strong tendency among the Pentacrinidæ toward the formation of essentially comatulid types. Such forms as those described above need but a fusion of the columnals, and an increase in the number and specialization of the cirri to make very fair Comatulæ.

Another feature which is not of great importance but nevertheless is somewhat suggestive of a similar derivation is the distinctly pentagonal section of many of the fossil comatulid centro-dorsals. This, for instance, may be noted in *Antedon* (*Solanocrinus*) *scrobiculata* (Pl. 8, fig. 3), in *Antedon depressa* (Pl. 8, fig. 8), and in many other fossil comatulids as figured by various authors. In the case of *A. scrobiculata* it is further to be noted that the cirrus sockets have an alternating "biserial" arrangement which points rather strongly to the conclusion that each successive cirrus on any given face of the centro-dorsal pertains to a distinct columnal. The pentagonal cross-section of such centro-dorsals may be held as resulting from secondary changes as induced by the presence of cirri, but comparison of these centro-dorsals with subglobose or bowl-shaped types seems to indicate that this may not necessarily be the case. Indeed the tendency toward modification of the shape of the centro-dorsal points rather toward the acquisition of a quite dissimilar type of organ.

It is not impossible that we may look among the species of *Millericrinus*, as defined by de Loriol, for ancestors of certain comatulid lines. This genus, as defined by de Loriol, contains many highly divergent types which at best may not be held as congeneric. Certain species tend toward *Apiocrinus*, which was doubtless derived from these forms, while others simulate in a marked degree members of the *Pentacrinidæ*. The genus is not as far removed from the Pentacrinidæ as is currently held, but whether these strikingly similar types represent members of quite distinct phyletic lines or are the result of convergence it is impossible to say. The evidence certainly points to a common ancestor not far removed. Taking *Millericrinus* in its accepted sense one might explain the petaloid markings of certain Comatulæ, as noted above, as the result of derivation from

this genus, for many of the species referred to *Millericrinus* have such a type of articulation. A careful examination of these forms may prove that they are after all referable to the Pentacrinidæ rather than to the Apiocrinidæ. The high degree of differentiation of the proximale in certain species of *Millericrinus* may indicate a tendency within the genus toward the formation of Comatula-like types by a disruption of the column immediately distad to this ossicle, after the manner of *Thiollericrinus*. Such a type of structure has already been noted in the case of *M. prattii*, although cirri were not acquired by this form.

Relationships of the Comatulæ.—Having briefly shown some of the reasons for assuming that the Comatulæ represent terminal members of a number of genetic lines, it may be well, broadly, to indicate the relationship of these forms to the Crinoidea at large. Bather and other authors have referred the Comatulæ, together with a number of other post-Paleozoic Crinoidea, to the Flexibilia. For the reception of this assemblage Bather has erected the Grade Pinnata. I believe that the Pinnata should be transferred bodily to the Order Inadunata. The presence of a persistent proximale, if there be such a columnal, has certainly not been established in the case of these forms, as has elsewhere been pointed out. On the other hand, the structural affinities of these organisms seem to lie far more with the Inadunata. Among all the known post-Paleozoic Crinoidea there is an essential unity of structure that points strongly to a not widely diverse origin. The ancestors of these Crinoidea may not, I think, be found in any known Paleozoic genera, but must be sought in early Mesozoic or late Paleozoic forms of minute dimensions.

TYPE 2.

The genera referable to this group probably constitute the only Crinoidea that maintain a truly eleutherozoic existence through their own exertions as freely swimming organisms. With them detachment from the column comes at a very early stage and results, as I hold, in the complete loss of that organ. The space inclosed by the proximal circlet of plates—either basals or infrabasals—through which the axial organs passed in the stalked ancestral forms is closed by a pentagonal plate, to which Bather has applied the name "centrale." Concerning the nature and origin of this plate it will be necessary to go into considerable detail. One of the most curious features about these crinoids is their apparent lack of antecedents. When first seen they are full-fledged pelagic types of a most remarkable degree of specialization, and it is a matter of exceeding difficulty even approximately to predicate the nature of their progenitors except in a very broad way.

The three genera constituting this group have been described and illustrated so adequately by various authors that it will scarcely be necessary to give any description of the forms other than may be required in a consideration of the broader aspects of certain structural features here discussed. Of prime importance in a consideration of these types is the question of the origin and homologies of the central apical plate, or centrale, which has been the subject of a considerable amount of speculation. This topic bears largely not only on the structure and relationships of these three genera, but also on many broader morphologic and taxonomic questions.

Bather on the "centrale."—Bather (1896, p. 979), in speaking of the centrale of *Uintacrinus*, says:

> The centrale is pentagonal, but in specimens examined not quite regular * * *. It is perfectly smooth, showing no signs either of a stem-attachment or of partition into more than one original element. Its homologies are therefore doubtful, as its structure and position permit it to represent either a relic of a stem or a fused infrabasal circlet, or even, as some would have it, an additional element altogether, to which the name "dorsocentral" might strictly be applicable. I have recently given reasons for rejecting the term and the idea "dorsocentral." Which of the other alternatives be correct is to be decided, if at all, by reference to the affinities and origin of the genus, as to which we are at this stage of the inquiry quite in the dark.

Referring to the group comprising *Saccocoma*, *Marsupites*, and *Uintacrinus*, he says that the central apical plate may originate in three ways (1896, p. 997):

> One may say, if one chooses, that in *Saccocoma* this represents the fused basals and in *Uintacrinus* the fused infrabasals; but in *Marsupites* it must be something else. Or one may say that in each case it is the same element, be it the proximal stem-ossicle (which some erroneously call "centrodorsal") or the distal stem-ossicle (which some, seeking an homology, have called "dorso-central"), or perhaps a new plate altogether, a simple supplementary plate developed to fill up the gap left by the disappearance of the stem. One might argue forever; there is no evidence. The one obvious fact is that such a central plate is found in three different forms, all of which were free-swimming, and unlike all other crinoids in showing absolutely no trace of a stem. It is therefore not safe to ascribe to the central plate any morphological significance or to give it any name other than "centrale."

In 1900 (1900, p. 135) Bather modified his statement in regard to the nature of this plate in *Uintacrinus*.

> * * * in *Uintacrinus* and *Marsupites* it represents neither basals nor infrabasals, but may be the proximale, or the supposed distal columnar plate ("dorsocentral"), or a new supplementary plate.

Springer on the "centrale."—Springer (1901, p. 22), in discussing the centrale of *Uintacrinus*, quotes the statements made by Bather in his paper on *Uintacrinus*, and seeks (1901, p. 28) to arrive at a more definite conclusion in regard to the origin and homologies of the plate. It will be noticed that he deals only with the suggestions of Bather as presented in his *Uintacrinus* paper and not as subsequently modified in Lankester's Zoology. He says in part (p. 28):

* * * it can not be (1) the fused infrabasals, because it is found here coexistent with them, a distinct element, situated within their circlet. There are thus left the other possibilities, viz: (2) That it is the representative of the proximal or distal stem ossicle; or (3) "a simple supplementary plate developed to fill up the gap left by the disappearance of the stem."

To the second and third hypotheses he objects (p. 28) on the ground—

That the centrale is located within the circlet of infrabasals, and abuts against them by their *inner* faces, instead of by their outer or dorsal sides. It does not envelop or conceal the infrabasals, as the proximal columnal does in pseudo-monocyclic forms; nor the basals and radials, as the representative of the stem in the Comatulæ usually does, although there is an exception to that in the case of certain living species of *Actinometra*, and in many fossil Comatulæ. On the other hand, the orientation of the centrale is precisely as the stem should be; i. e., interradial when the infrabasals are present, and radial when they are not. And the orientation is strongly against the third of the above suppositions. For the gap left by the disappearance of the stem, and to be filled up by stereom, would be the axial canal piercing the base of the calyx at the center of the basal or infrabasal ring. This would be radial in the latter case and interradial in the former. A supplemental plate developed to fill up this space should have the same orientation; but this is just the reverse of what is exhibited by the centrale. It seems to me, therefore, that the argument is decidedly in favor of the view that the centrale is a relic of the stem of the Stalked Crinoids, if not, indeed, of the pedunculate stage of *Uintacrinus* itself.

This last statement is explained more at length on page 59, where he implies that the centrale is a modified proximale as in *Millericrinus prattii*, *Actinometra*, and other Comatulæ.

Probable origin of the centrale.—At this point I wish merely to consider the second and third possibilities given by Bather, and the objections raised in regard to them by Springer. Against the hypothesis that the plate represents the proximal or distal stem ossicle, he brings the argument that the centrale lies *within* the circlet of infrabasals, and "abuts against them by their inner faces, instead of by their outer or dorsal sides, etc." This objection I consider insuperable, although Springer, as above quoted, apparently does not, considering such a solution of the problem the most reasonable one. In no case do we know of the proximal columnal taking part in the dorsal cup except as a proximale, fusing with the infrabasals which it overlies. Nor can we readily imagine a proximal columnal, resting on the outer faces of the infrabasals, consolidated into a plate which is squeezed into an opening of the size of the axial canal with which, as a columnal, it was itself perforated.

An obvious argument against this last conception is that the separation of the crown and stem took place very early in the ontogeny of the animal, and that the proximale, now the centrale, enlarged but very slightly or not at all in the subsequent growth of the crinoid. Even at this early stage, however, the proximale would have had to fit into an opening smaller than itself. The cases among *Actinometra* where the cirri are lost, and the centrodorsal by partial resorption

becomes rounded and flush with the adjacent plates (Pl. 6, figs. 9 to 11, and Pl. 5, figs. 10 to 12), rests on an entirely different footing. Here the proximale is probably fused with the infrabasals, and partially with the basals. Again, the centrale of *Uintacrinus* is very thin, and shows no sign of a central perforation in either a dorsal or ventral view. Had there ever been one, there would most certainly have been a decided thickening of the plate, which, even if partially resorbed in the adult, would be indicated in very young specimens. Such, however, is not the case.

Now let us turn to the third hypothesis, which is so improbable on the grounds of orientation. According to Springer, in the passage quoted above, a supplemental plate should conform to the angles of the axial canal, being radial in a dicyclic form and interradial in a monocyclic individual. This is absolutely at variance with the observed condition of affairs, as is shown on Plate 9, figures 1 and 11.

Carabocrinus, a dicyclic Inadunate from the Ordovician has a decidedly pentalobate axial canal, which is radial as should be the case in a dicyclic form. In a specimen from which the column had been broken, careful cleaning shows that the infrabasals are distinctly invaginated by the axial canal at their lower margins. It has been my good fortune to obtain an adult specimen of *Carabocrinus radiatus* from the Trenton limestone of Canada, which, probably through some accident, completely lost its column during life. That this separation of stem and crown occurred late in the life of the individual, there can be little doubt. The stem-cicatrix on the inner edges of the infrabasals is distinctly marked, and is of considerable size. A comparison of the diameter of the stems of other specimens, with the diameter of the cicatrix in this individual, indicates that the crinoid could not have been a great deal smaller when it became free than it is at present. In this specimen we find a small centrale within the infrabasal circlet. In this case there was no possible chance of the proximal columnal becoming transformed into a centrale. The proximal columnal was fully formed, and over twice the diameter of the opening left between the infrabasals. Moreover it lay on the *outer* faces of these plates. Such a columnal could scarcely be imagined by the exercise of ever so much ingenuity to become a comparatively minute plate, lying *within* the infrabasal circlet, and abutting against the *inner* faces of these plates.

Granted then that this centrale could not have been formed from the proximal columnal, the question naturally arises as to what it really is. The only possible answer is that it is an entirely new element, functioning as a plug to stop up the axial canal. A hint as to the possible derivation of this plate is given by Carpenter (1884, p. 34). In *Bathycrinus*, *Rhizocrinus*, and *Pentacrinus* there is in the lower inner portion of the dorsal cup a sort of plug formed of

calcareous matter. In these forms, this plug only extends to the tops of the basals, and is of rather loose texture. It shows, however, the tendency of calcareous matter to be deposited in the basal portion of the cup, which, in case of the detachment of the crinoid from its column, could readily be formed into a solid plug. A relatively slight extension of this calcite-depositing tissue would completely fill the axial canal, and form a plate which on the exterior would be flush with the plates of the proximal circlet. Thus it is probable that in the case of *Carabocrinus* at least, the centrale was formed from within, outward.

The most astonishing thing about this plate in *Carabocrinus* is that, contrary to all expectations, it does not form a stellate plug which merely fills up the axial canal, and the angles between the infrabasals, but actually constitutes a pentagonal interradial centrale. The orientation of a central, apical plate, then, if it lies within the proximal circlet of plates, and "abuts against them by their *inner* faces" is of absolutely no importance. The centrale in all cases conforms to the angles of the adjacent plates and not to the lobes of the axial canal. Another instance of a plate conforming to the surrounding plates has already been given in the case of *Antedon*. Here we find in the early stages that the proximale is pentagonal, and radial in position, its shape being controlled by the basals. Later, when the centrodorsal has overgrown the basals, the shape of the plate is governed by the general contour of the calyx and the presence of cirri. These factors are of course, not at all of the same nature as the one that controls the plate when it lies *within* the proximal circlet. In the latter case it is the absolute lateral contact of the adjacent plates that governs its form.

The centrale of *Uintacrinus*, I take it, was an entirely new element, formed much in the same manner as the plate in *Carabocrinus*. The presence of infrabasals and the centrale in some of the individuals precludes the possibility of its having been formed by the fusion of the infrabasals.

Significance of both mono and dicyclic bases in Uintacrinus.—The presence in *Uintacrinus* of apparently both dicyclic and monocyclic types has been considered as of the utmost importance by Springer and others, as conclusively showing the unimportance of the features upon which Bather has made his main divisions of the Crinoidea. Mr. Springer's views on the subject may best be explained by a quotation from his work on *Uintacrinus* (1901, p. 30):

> If the two forms of base represented by text figures 1 and 2 had been found in specimens otherwise separable, they would, under Mr. Bather's arrangement, have been unquestionably referred to different genera, families, orders, and subclasses. Considering the apparent identity of these forms in every other point of structure, coupled with their mode of occurrence and association, I do not see how any such separation can possibly be made in this case. We therefore have apparently to deal with a case

of individual variation, as to this supposed primitive character, within the limits of a species. That is to say, in this species, living in the same locality, having the same environment, floating in the same mass, certain individuals matured to represent one stage of larval development, i. e., with infrabasals, and others in another stage, i. e., with basals only. In short, they are the two supposed distinct types, Monocyclica and Dicyclica, occurring in both young and adult of one and the same species.

Why is not the centrale in the so-called "monocyclic" type of *Uintacrinus*, merely the primitive centrale of the dicyclic type to which the infrabasals have become fused? Springer, in his memoir on *Uintacrinus*, argues against the transmutation of one form into the other on various grounds. His arguments may best be brought under several headings, and so discussed. All page references are to his work on *Uintacrinus* unless otherwise stated.

On page 25 he says: "The differences presented by forms M and D are not correlated with any other characters. They have no apparent relation to size or maturity of the specimens, and therefore could not have been the result of differences in individual growth." Against this assertion I can offer no more convincing proof than Springer's own subsequent statements: "There is no reason, based upon any characters exhibited by these specimens, for any inference as to one being prior in development rather than the other, unless it is the greater prevalence of Form D among the young individuals." This prevalence of Form D in the young, we find to be very striking indeed, and is of the utmost significance. On page 34 we find the relative proportion of Form D among the young and adult specimens to be as follows: "Among specimens measuring under 25 mm. across the calyx, 75 per cent are dicyclic; while among those of maximum size—50 mm. and over—the proportion of dicyclic is about 40 per cent." In the face of these figures, he continues (p. 34): "If there were a tendency to develop by individual growth into either form, then we ought to find practically all the adult specimens belonging to that form; and the same thing would be true if the transition took place during the larval stage."

It is true that we do not have all the adults, or 90 odd per cent of them, "monocyclic," or all the young "dicyclic," nor should we expect it. A change from 25 to 60 per cent, which expresses the change in percentage of "monocyclic" forms in the young and in the adult stage, is rather startling, however. As a matter of fact, the change is slightly less than that just given, based on Springer's figures given below. On page 86 in a table that recapitulates the data bearing on the number of interbrachial plates and the character of the base, we find that out of a total number of 82 individuals measuring less then 25 mm. in diameter, but 20 are "monocyclic." This gives us a percentage of a trifle over 24 per cent—not 23 as given in this table, where the percentage of "dicyclic" specimens is set down as 77 per cent. Among individuals having a width of

calyx of from 61–75 mm., 59 per cent are monocyclic. The high percentage of Form D in the young and the low percentage of the same type among the adult specimens is evidence amounting almost to proof that there is a change in the structure of the base in the ontogeny of the animal.

It may be argued, and this seems to be the attitude assumed by Springer, that if the change from dicyclic to "monocyclic" took place in the ontogency of certain individuals, the same process should be effective in all cases. It is highly unreasonable to look for the transmutation of one type into the other in the case of each and every crinoid. Such a universal acquisition of this character could only obtain where the tendency had become most thoroughly impressed upon the race through its acquirement by a great number of successive generations. In *Uintacrinus* the tendency toward the fusion of infrabasals with the centrale had its inception at no very remote date. This is clearly shown by the fact that the period of fusion, although variable as to the time of occurrance, in most cases comes rather late in the ontogeny of the animals.

An examination of the tables in Mr. Springer's monograph on pages 78–85 will show even more clearly than the percentages already given how gradually and at what different stages in development the change from one form to the other took place. These facts prove that the fusion of the infrabasals was a comparatively new thing, and as a result was not uniformly acquired by the different individuals. Everywhere we find that certain individuals are more accelerated in development than others. A structure that appears in one *Uintacrinus* when but 25 mm. or less in diameter might well be retarded in another until the animal had attained its maximum growth. Another factor that may be considered is that of sexual difference. It is a matter of common knowledge that one sex is frequently more accelerated in development than the other, and I have been assured by Prof. R. T. Jackson that such is the case among living Echinoderms, at least in some forms. This differential sexual acceleration I would not lay much stress upon for the reason that probably the females so greatly exceeded the males in number that any such difference would but slightly affect the general result. This probable preponderance of the females over the males will be discussed later.

At any rate we can readily conceive that such a fusion of the centrale with the infrabasals, taking place first in the adult crinoids, gradually was pushed back farther and farther in the ontogeny of the animals, and, finally, may have taken place immediately upon the formation of the centrale, following the detachment of the crinoids from their stems. This acceleration in development, resulting in the acquirement of a "monocyclic" base at various stages of growth answers perfectly the objection raised by Springer on page 26 in

regard to the relative size of the centrale. We find in *Uintacrinus* that the centrale varies considerably in size, apparently irrespective of whether it occurs in Form M or D, or of the size of the individual to which it belongs. Apparently, however, the centrale in Form D is "often very small." In some cases where fusion does not take place the centrale increases somewhat in size. There is indeed no good reason why the centrale in *Uintacrinus* should not show variation in size in different individuals. In *Marsupites* we find that the central apical plate, which in the young must have been quite small, became relatively enormous in size. The increase in size of the centrale in *Uintacrinus* is similar in kind, if not in degree, to that shown by *Marsupites*. The variation in size of the centrale in Form D may readily be explained. If the fusion of the infrabasals with the centrale took place early in the life of the individual, a small plate would have been formed of necessity. This might or might not have increased in size during the subsequent growth of the animal, the size being again merely a matter of individual variation. If the infrabasals fused with the centrale later in the life of the crinoid, as in some cases they certainly did, the resultant plate would have been of comparatively large size. This plate might still be added to, making it even larger. It seems to me that the foregoing arguments explain the variations in the size of the centrale in Forms M and D, and the occurrence of both types of structure in young and adult individuals, features upon which Springer lays particular stress on page 34 and elsewhere.

In regard to the possession of the two types of base by *Uintacrinus*, Springer, on page 25, says: "It is not a case where the infrabasals are concealed, or are more or less perfectly or imperfectly developed, or are used with some other element, as in some forms which Bather calls pseudomonocyclic. For here Wachsmuth and Springer's law of alternate arrangement of the elements of the Crinoid skeleton strictly prevails." As I have previously shown, the orientation of the centrale is of little or no importance, being dependent entirely upon the character of the surrounding plates. In Form D the centrale fits into the angles between the infrabasals, and is, therefore, interradial. In Form M the centrale (consisting now of the original centrale, to which the infrabasals have fused) adjusts itself to the angles of the basals, and is, therefore, radial. Springer also uses this argument against the possiblity of the fusion of infrabasals and centrale at the bottom of page 30. It is curious to note in this connection, that on page 32 in considering the possibility of a fused condition of centrale and infrabasals he says: "A coalescence or fusion of the infrabasals with the centrale would not be subject to the same objection on the ground of orientation. The resulting plate would be radial, as it should be in a monocyclic form."

Mr. Springer, on page 31, considers that the change from one type to the other might have taken place in one of three ways:

1. The resorption of the infrabasals in Form D.
2. The intercalation of infrabasals in Form M.
3. The coalescence of the infrabasals with the centrale.

Although I do not believe that the change was brought about by the second process, and can accept the first hypothesis only as a partial explanation, either is a *possible* explanation for the facts as we know them. Therefore it is best to consider the arguments for and against both before taking up the discussion of the third, which, as before stated, I believe to be essentially the correct interpretation.

The argument brought against the first two hypotheses by Mr. Springer is that of the orientation of the centrale, which he considers an insuperable difficulty. As shown above, the centrale is dependent as regards its form on the plates surrounding it. To show what a simple matter it would be to change the orientation of the centrale by the intercalation of infrabasals consider first figure 11, Plate 9, a typical Form M, with an unusually large centrale. Here the centrale is pentagonal and radial. Now, at the apices of this pentagon suppose we introduce five minute infrabasals. To allow the introduction of these infrabasals, however small, there is a synchronous resorption of each apex, which becomes more marked with the increase in the size of the infrabasals. We now have a decagon, such as is beautifully shown in figure 3, Plate 9. If the infrabasals continue to grow there will be a corresponding resorption of the centrale along the surfaces in contact with the infrabasals. It is obvious that soon the infrabasals will meet laterally, and the inclosed centrale instead of being a radial pentagon or decagon will be transformed into an interradial pentagon, resulting in a form like figure 2, Plate 9. So far as orientation is concerned this hypothesis is perfectly sound. If we reverse the series outlined above we can see how the form of the centrale can be altered from interradial to radial, if we wish to establish the validity of the infrabasal resorption theory. Here, starting with figure 2, Plate 9, let us consider that the centrale gradually enlarges. As it increases in size there is a concomitant resorption of the apical portions of the infrabasals. Before long we reach the decagon stage, represented by figure 3, Plate 9. If this process be continued but a short time longer these minute remnants of the infrabasals would disappear, their places being taken by the enlarged centrale. A very slight straightening of the lines of contact between the centrale and basals would give us a typical Form M, with a radial centrale. That such resorption and mutual readjustment of plates is quite possible will be shown hereafter at some length.

As shown above, Form D *could* be evolved from Form M, providing the requisite infrabasals were supplied. But where could these plates

come from? There are but two possible ways to account for their appearance. In the first place, the plates might have arisen as absolutely new elements in a true monocyclic crinoid. This theory, as hereafter explained, I consider absolutely untenable. In the second place, if *Uintacrinus* were descended from a pseudomonocyclic form the infrabasals which in the ancestral type were practically obsolete, upon the assumption of an eleutherozoic existence, might have begun to appear as important elements of the cup. It is obvious that if we accept the theory of the intercalation of infrabasals we can not tell by which of these two processes the plates were formed.

I can not, however, in any way admit the possibility of the infrabasals representing absolutely new elements in the cup. In the first place, there is no logical reason for their existence. They add not at all to the efficiency of the crinoid, and among the Crinoidea we see little or no aimless variation. The sole possible excuse for their introduction would be the enlargement of the cup. The resultant amount of enlargement is palpably insignificant and could quite as well have been accomplished by the enlargement of the centrale and proximal plates, as in *Marsupites*. Again, the introduction of these new elements would necessarily result in a fundamental change in the nervous system. The change from a dicyclic to a monocyclic type of nervous system I consider quite within the range of possibility, but a reversal of the process offers insuperable difficulties. The essential difference between a dicyclic and a monocyclic crinoid can scarcely be emphasized too strongly. Certain it is that one form can only arise from the other as the result of a long evolutionary process, and it is quite inconceivable that, as would have to be the case in this instance, one type should be a mere mutant of the other.

Against the possibility of the enlargement of the minute infrabasals of a pseudomonocyclic type one can not make so strong a case. The uselessness of the proceeding is perhaps as good an argument in this case as in the preceding. One would certainly expect that with the assumption of a free-swimming existence and the formation of a centrale that the minute plates would fuse with the new element. This would only conform to the general tendency to be observed among nearly all crinoids toward the gradual elimination of the proximal circlet of plates as distinct elements.

How are we to explain such types of bases as are shown in figures 5, 6, 7, and 8, Plate 9? Obviously figures 5 and 6 may represent individuals in which three and four infrabasals have appeared, respectively. It is not so easy, however, to account for figure 7. Springer describes this specimen as having a double centrale and one infrabasal. We are not told, however, by what process two centrales could be formed. If the centrale represents the rudiment of the ancestral stem, could one individual have been the fortunate

possessor of two columns? Again, if, as I believe, the centrale merely represents a plate to fill up a gap—an entirely new element—why should two plates have been necessary to fill up one small opening? A glance at this figure will show clearly that such an explanation is quite out of the question. There is but one possible explanation of this base and that is a fusion of the plates. If there is fusion here we may expect it elsewhere. Under the discussion of the third hypothesis I shall deal with this coalesence of the plates in some detail. I wish at present merely to point out that we have every reason to believe that fusion among the plates did take place.

If we attempt to explain figures 7, 6, and 5 as cases where one, three, or four infrabasals only have appeared, the question involved is a far greater one than the mere explanation of the apparent vagaries of *Uintacrinus socialis*. It may be stated almost as a law that each of the circlets, composed either of basals or infrabasals, acts as a unit in evolutionary changes; that is to say, if, for instance, the tendency in evolution is toward an elimination of the infrabasals, all are equally affected. The plates finally become of so little importance as to be practically a negligible quantity, thus forming a pseudo-monocyclic type. Again, one or more of the plates of a circlet may not drop out, leaving the remainder to shift for themselves. Naturally certain plates of a circlet may be modified and become larger than the others, as is well shown by the basals of *Eleutherocrinus*, all five plates being represented. This rule, it seems to me, holds absolutely in regard to the presence or absence of plates. If one plate of a circlet be present, the other four are present, except in purely abnormal individuals. So here in *Uintacrinus* I do not believe it possible for one, three, or four infrabasals to be present and the others absent. Hence, any apparent reduction in number must necessarily be due to fusion. Of course, one may claim that all these specimens cited are abnormal, but as long as the structures observed can be explained as the result of a perfectly normal process, and, indeed, are exactly what we should expect to find, it seems rather unnecessary. As before stated, I believe that the change from Form D to Form M has been brought about by a fusion of the plates. At the same time more or less resorption took place, so these two processes will be discussed together.

On page 32 and following, Springer raises the following objections to the fusion theory other than those already discussed. In the first place, he has never seen a specimen in which the coalescence of infrabasals and centrale would result in the formation of a plate having the outline of the centrale actually found in Form M. The centrale in Form M is pentagonal, whereas the resultant plate he thinks should be stellate. In the following passage which I quote from page 32, the qualifying phrases, which I shall here place in italics, somewhat

spoil the force of the argument. "Among the 268 dicyclic specimens examined by me *I can scarcely point out one* in which the coalescence of the infrabasals and centrale would produce a plate having the same outline as the centrale has, or which would not be entirely distinct in shape from the centrale in *most* of the 275 monocyclic specimens in the collection." These irregularities in the shape of the centrale will be discussed later. At this point let me merely point out that in the case of *Carabocrinus* already cited we have a stellate opening to be filled, but the centrale which is formed is strictly pentagonal and, moreover, interradial.

It is a notable fact, although one which I believe has never been hitherto pointed out, that a permanent reentrant angle is an unknown quantity in a fully formed crinoid plate. This rule applies with equal force to a composite plate resulting from the complete fusion of two or more primary plates. Indeed, I hold that this rule is equally applicable to all Echinoderms. The forked radial of the Blastoidea will suggest itself to everyone as an exception to the rule. Even in this case, however, the exception may prove more apparent than real.

In the case of fusion among basals and infrabasals in crinoids the resultant reentrant angle formed between any two of the plates tends to fill out and make a straight face. At the same time there is a gradual resorption of the lower edge of the plate resting in the reentrant angle. Within a short time all traces of the reentrant angle disappear and a straight face results. Why this is so it is hard to say, unless it be that a reentrant angle is a source of weakness in a plate and is eliminated as rapidly as possible. A large number of examples of such filling up of reentrant angles might be adduced. An examination of a series of Camerata in which the basals tend to fuse into a solid plate will illustrate this condition admirably. In certain species where fusion has not become effective, or in young individuals, it is to be noted that certain of the radials, and frequently the proximal anal plate, if such be present, rest in reentrant angles formed by the basals. Upon a complete consolidation of the basals a pentagonal or hexagonal plate with straight faces is formed. Such a hexagonal disk as is shown in the genus *Megistocrinus* is here figured (Pl. 9, fig. 12). In other specimens of *Megistocrinus* it may frequently be observed that the anal rests within an angle formed by two of the unfused elements of the tripartite base.

The regular polygonal shape of such basal elements as is to be noted in the Camerata may only be accounted for on the basis of fusion and subsequent filling of reentrant angles. Where before there was a reentrant angle between two plates, after such fusion we find a straight face. This change necessarily requires not only

a filling out of the reentrant angle, but a concomitant resorption of the proximal portion of the plate which rests within the angle. If we take a monocyclic crinoid with a tripartite base we do not say that there can only be three basals present, because there are no signs of sutures or reentrant angles, and we can only see three elements. If such a statement can not be applied here, wherein are we justified in making the same assertion in regard to the proximal circlet of *Uintacrinus?*

On page 33 and elsewhere Springer states that there is no evidence of fusion. Why does not his Plate 2 show practically every step in such a process? On Plate 9 will be found reproduced the important stages figured by him. Figure 7 shows clearly that fusion of one sort or other must have taken place. It is evident that there is a single unfused infrabasal and one plate consisting of two fused infrabasals. It is not necessary at this point to determine the composition of the third plate, although we know that it must be either the centrale alone or the centrale with which the other two infrabasals have fused. The important fact is that there is a tendency toward fusion among these plates just as we found that there was a similar tendency among the plates of the proximal circlet of other crinoids. If there be such a tendency toward consolidation, is it not highly probable that the plates will not only fuse among themselves, but also with the centrale? If so much be granted, it is very easy to explain the various bases figured, which are otherwise so puzzling.

Figure 11 shows the regular "monocyclic" base with the centrale of maximum size. Figures 1 and 2 show the normal dicyclic base. In figure 5 we find that one infrabasal has fused with the centrale. The four other infrabasals are present, three being relatively small, while the other is quite large. In figure 6 we see that two of the infrabasals have fused with the centrale. Figure 7 shows a modification of the process. Here the centrale has fused with two of the infrabasals, the resultant plate probably being represented by the largest plate of the three—that on the upper left-hand side. In addition, two of the infrabasals have fused, forming the plate next in size. A fusion of the centrale and two infrabasals and the remaining unfused infrabasals would most certainly give the form represented in figure 8. A further fusion of these two elements would result in an irregular plate, which would gradually acquire a more symmetrical form by a process of accretion in some parts and resorption in other parts, combined with similar processes acting on the adjacent faces of the basals.

Apparently the coalescence of the infrabasals and centrale took place in no definite order. In figure 7 two infrabasals fused together, while the centrale fused with two others. Another variation is to

be noted in figure 3. Here the infrabasals are greatly diminished in size, while there is a corresponding increase in the size of the centrale. Here there seems to be no possibility of a fusion between the members of the infrabasal circlet. In case fusion had taken place subsequent to this stage the infrabasals would have united directly with the centrale. In figure 5 there was a similar reduction in the size of the infrabasals before, or, perhaps, during, the process of fusion. The tendency was toward the elimination of the infrabasals as distinct elements, and whether the result was obtained by the simple fusion of the plates concerned, irrespective of the order in which such fusion took place, or by the partial resorption of the infrabasals and their subsequent coalescence with the centrale, was of little moment.

Springer styles all those apical plates that meet interbasal sutures by more than one angle, "centrales." Thus in figure 8 we find *two* "centrales," and in figure 7 two centrales and one infrabasal. Such types he describes as having a double centrale. As previously stated, Springer does not attempt to explain how two centrales could by any chance have been produced in an individual. He merely states that "all these irregular cases are rare and exceptional, and constitute mere individual variations." Two such plates could certainly not represent a "proximal or distal stem ossicle." If a gap existed to be filled, one plate would have been formed—not two. The only other possible explanation for a "double centrale" is that one of these plates is composed entirely of fused infrabasals, and the other made up of the primitive centrale to which one or more infrabasals have fused.

Springer calls attention to the fact that in the case of figure 6 the centrale is both interradial and radial. Hence it follows according to the law of Wachsmuth and Springer, which "strictly prevails," that this individual is at one and the same time monocyclic and dicyclic. This is obviously impossible. The specimen *does*, however, combine features typical of forms M and D as shown by *Uintacrinus*. This same plate beautifully illustrates my contention that the shape of the centrale is entirely dependent upon the plates surrounding it. On one side the centrale rests against three infrabasals, and conforms to the angles between these plates. As a result, on that side it is interradial. On the other side it has fused with the other two infrabasals, and after a process of mutual adjustment between itself and the basals, one complete and two incomplete sides of the pentagon to be have been formed, the inclosed angles conform to the basals and are radial in position.

Inasmuch as Form M in *Uintacrinus* is not truly monocyclic, we may well pass over the last objection of Springer on pages 33 to 34 in regard to the supposed change in orientation of the chambered

organ. This organ would not necessarily be changed in any way. The loss of the stem would doubtless result in a more or less complete coalescence of the lobes of the chambered organ, much as we find in the case of *Actinometra* and *Antedon*. The mere subsequent fusion of the infrabasals with the centrale would probably in no wise affect the organ. Certainly there would be no occasion for a transformation of one form into the other involving "in addition to the change in orientation of the centrale, a revolution of the chambered organ, and an extension or shortening (as the case might be) of the downward prolongation of the axial nerve-cords."

How important a part resorption of the infrabasals has played in the transmutation from one form into the other must always remain a moot question. It is perfectly possible that the change might be effected by this process. If in a specimen like figure 3 the infrabasals become progressively smaller and smaller it is evident that before long they will entirely disappear and their place be taken by the centrale. A very slight resorption of the proximal faces of the infrabasals and a corresponding increase in the size of the centrale would result in a typical centrale of Form M. It would certainly be difficult to prove in advocating this theory that in the final stages of the process the remnants of the infrabasals did not fuse with the centrale. The question is apt to remain an open one indefinitely.

The fusion observed in some specimens, as pointed out above, between the infrabasals themselves and the infrabasals and the centrale certainly shows that there was a tendency toward coalescence. If then we have a well-marked tendency in this direction, and if all the known facts appear to warrant rather than discourage such an assumption, we should feel quite justified in considering the fusion theory the more probable one, with resorption playing a minor or subsidiary part.

On page 35 Springer offers three alternatives to explain the presence of Forms M and D in the one species:

1. That from the eggs of either a monocyclic or dicyclic crinoid both forms were indiscriminately hatched.

2. That they hatched in one form, with a tendency in the larva to develop into the other, which tendency irregularly became effective in some individuals and ineffective in others.

3. That after the larval stage, by some process of addition, subtraction, or consolidation among the hard parts of the test, a dicyclic crinoid was transformed into a monocyclic or *vice versa*.

From the discussion given above we may offer here an explanation compounded in part from the second and third alternatives of Springer.

The larvæ were certainly dicyclic and became free-swimming at an early age. When a crinoid became detached from its stalk, a

calcareous plug was formed to fill up the opening through which the axial canal had formerly passed. The tendency in the development of the animal, so far as the base is concerned, was now toward an elimination of the infrabasal circlet as composed of distinct elements. This took place probably as a result of the consolidation of this newly formed centrale with the surrounding infrabasals. The consolidation "irregularly became effective in some individuals and ineffective in others," dependent, as explained above, upon the fact that some individuals were more accelerated in development than others. This consolidation of the proximal circlet is a tendency to be observed among all crinoids, and especially is it to be noted in free-swimming types such as, for instance, *Agassizocrinus* and some species of *Edriocrinus*. In such recent forms as *Antedon* and *Actinometra* the infrabasals are practically obsolete and fuse very early with the proximale. Even the basals, which to all intents and purposes have now become the proximal circlet, are affected by the same tendency, fusing to form the so-called "rosette." It might well be that if given sufficient time the basals of *Uintacrinus* would in turn be reduced and fused with the centrale. Indeed figure 9 seems to show that such a process had already begun. Here the presence of apparently four basals suggests the fusion of two of the plates, although it is obvious that this condition of the plates may be purely abnormal.

It is evident that Bather's arguments in favor of his classification have yet to be refuted. Whether the change from Form D to Form M or *vice versa* took place by the intercalation of infrabasals on the one hand or their elimination on the other is of little moment so far as this particular question is concerned. If there has been an elimination of the infrabasals by fusion or resorption, the resultant form still remains a dicyclic crinoid, or at most may be styled a "pseudomonocyclic" form. In case the infrabasals have made their appearance in Form M it will be impossible to prove that they do not represent the nearly obsolete plates of an ancestral pseudomonocyclic crinoid. In this case the plates that had come to assume an insignificant part in the makeup of the crinoid were brought back to a state of comparative prominence under the stimulus of changed conditions of life. Against this hypothesis it may be argued that in typical Form M absolutely no trace of infrabasals may be seen. This objection carries little weight, however, as the infrabasals in the ancestral form may well have been present only in the larval stage and have become quite obsolete in the adults. Whatever the process, then, all one has is a change either from pseudomonocyclic to dicyclic, or from dicyclic to *apparently* monocyclic or pseudomonocyclic types.

Probable derivation of Uintacrinus.—Among all known crinoids *Uintacrinus* possibly stands as the form best adapted to meet the

requirements of an eleutherozoic existence. As a result of this high degree of specialization it is difficult, if not impossible, to pick out any specific structure and use it as the basis of comparison with any special group of crinoids in the hope of proving genetic relationship. The structure of the tegmen; the exocyclic mouth; the thinness of the plates of the cup; the large visceral cavity, made possible by the fixation of pinnules and introduction of interbrachials; the length of the arms; the presence of syzygies; all these are modifications for which a free-swimming existence is directly responsible. In order then to arrive at any sort of a satisfactory conclusion in regard to the relationships of *Uintacrinus* we must consider the form stripped of its special modifications. To be sure, with these gone we have little left, but even that fact is of considerable importance.

The exocyclic tegmen illustrates, I believe, an accentuated bilateral symmetry induced by a pelagic existence. The marked regularity in the swimming movements of eleutherozoic types such as to be noted in living Comatulæ, unquestionably tends to bring about a bilateral symmetry on the part of the organisms.[1] Among other Echinoderms, notably the Eleutherozoa, the acquisition of a secondary bilateral symmetry is too well known to warrant extended comment. Nor can the flexible tegmen be taken as positive evidence of relationship with any special group. This, too, is simply an expression of a free-swimming existence—a pliant disk making for greater mobility and consequent arm freedom. The arms themselves again exhibit great specialization, but there is nothing in their structure which might not be independently acquired. The fixation of pinnules, although characteristic particularly of the Camerata, nevertheless need not be restricted to that group. In *Calamocrinus* and *Actinometra*, for instance, we find a partial incorporation of the arms and pinnulæ into the calyx, and also in *Dadocrinus*, as pointed out by Bather. In *Uintacrinus* such incorporation was the logical thing. The interbrachial system does not, I think, show marked affinities with any group. Its great irregularity, if anything, rather argues against a close relationship with the Camerata.

[1] Mr. A. H. Clark has proposed an interesting hypothesis to explain the exocyclic disk of the Comatulæ. According to him, this type of tegmen is evolved as the result of the feeding habits of the crinoids. Mr. Clark says that those forms with exocyclic disks constantly keep their digestive apparatus filled with bottom mud, from which they extract the nutritive material. Such feeding habits necessitate the possession of an unusually long gut, as one finds in animals which feed in this manner. When one considers the limited capacity of the body cavity it is obvious that such an increase in the length of the gut must result in a coiling of that organ. Concomitant with such coiling Mr. Clark maintains that the orientation of the disk changes. Such an explanation is equally applicable to *Uintacrinus*, Mr. Clark holds, though here it is not bottom mud but surface plants as a food supply to which the animal must adapt itself. This explanation seems a possible one in the case of *Actinometra* at least, and is an alternative explanation constantly to be borne in mind.

The feeding habits and food of endocyclic and exocyclic forms should be noted with care. In the case of a number of *Actinometra japonica* the included food of which I have examined, I found no evidence of bottom sediment. The intestine content was composed almost wholly of comminuted animal matter.

Springer seems to favor descent from the Flexibilia. On page 58 he records the tendency among certain Flexibilia to separate from the stem just below the proximale. If the proximale be true to its definition it will always remain, fusing with the proximal elements of the cup. In *Uintacrinus*, as shown above, this condition can not obtain. As long then as only those forms having a persistent proximale are to be referred to the Flexibilia, so long must *Uintacrinus* seek relationship elsewhere. The Camerata as the ancestral stock, as suggested by Jaekel, is a proposition scarcely to be considered seriously. By a process of elimination, then, we have narrowed the field down to the Inadunata, in this agreeing with Bather. To attempt to fix the line of descent any more definitely is, I think, at the present state of our knowledge, somewhat premature.

The stalked Inadunata ancestor should, I think, unlike *Dadocrinus* chosen by Bather, be a distinctly dicyclic form, not pseudomonocyclic. The apparent elimination of the infrabasals in some specimens of *Uintacrinus* is a feature acquired very late in the evolution of the genus. In this connection the possibility of the infrabasals of a pseudomonocyclic form regaining their former importance as elements of the dorsal cup, upon the loss of the stem, is a consideration not to be lost sight of, as pointed out above. In such a case, however, it is very difficult to see why the tendency shown by *Uintacrinus socialis* toward a coalescence of centrale and infrabasals, which is merely an expression of the general trend of all crinoids toward a more or less complete elimination of the plates of the proximal circlet as distinct elements, should show itself so late in the developmental series. One would think that in their almost completely atrophied condition in the pseudomonocyclic form, the infrabasals would at once fuse with the new element, the centrale, rather than remain as minute independent plates. Whatever be the genetic line that evolved *Uintacrinus* it is probable that we shall ultimately come to a type that will serve as a common ancestor for both *Dadocrinus* and *Uintacrinus*. This type again may serve equally well for many of the phyletic lines that flourish in Mesozoic and later times.

Springer (1901, p. 55) objects strongly to the placing of *Uintacrinus* in the Inadunata. In speaking of the relationship of *Uintacrinus* to *Dadocrinus* he says: "In the essentials of structure upon which the great groups of Camerata, Inadunata, and Flexibilia have been distinguished, *Uintacrinus* seems to me far more widely separated from this group than from the others." In regard to its positive relationships he says: "It must be evident that the line of derivation of *Uintacrinus* will have to be considered in connection with the Comatulæ. Whatever its ancestry may have been, it is quite plain that one of its near relatives was *Actinometra*." It is mainly on the evidence of similarity of structure as induced by the mutual possession of

exocylic disks that this close alliance with *Actinometra* is predicated. These features as elsewhere noted I believe to be purely secondary and induced by an eleutherozoic mode of life. *Actinometra* and *Uintacrinus* I do not believe we may safely hold to be more closely related than as having descended from a common pre-*Dadocrinus* ancestor.

A. H. Clark (1909 *b*.) in placing *Uintacrinus* systematically, groups the Uintacrinidæ and Marsupitidæ together under the "Comatulida Innatantes." His definition follows:

> Comatulida Innatantes: Pelagic comatulids in which the basals are not metamorphosed but form an integral part of the body wall; the infrabasals are not united with the central plate, but usually form part of the body wall; occasionally, through individual variation, they are absent; there is no evidence of attachment at any stage, so that their central apical plate may possibly represent the dorso-central instead of the centro-dorsal of other comatulids. The plates of the calyx, which is very large and more or less globular, are very thin.
>
> Included families: Marsupitidæ; Uintacrinidæ.

This treatment is but slightly better than the time-honored and discarded custom of placing the two genera into one family. It is to be noted that he follows Springer in placing *Uintacrinus* with the Comatulæ. Springer, however, while placing *Uintacrinus* among the Comatulæ, and consequently in his opinion, in the Flexibilia, retains *Marsupites* as a well-defined Inadunate.

Ecology of Uintacrinus.—There can be little doubt but that *Uintacrinus* was a pelagic type. Its extreme modifications to adapt it for such an existence, and above all its lack of prehensile cirri or other organs by means of which it could attach itself to extraneous objects, coupled with the extreme length and flexibility of its arms, are almost conclusive proof that such is the case. Such forms as *Agassizocrinus* and the free *Edriocrinus* which likewise lacked cirri, but which were decidedly not fitted for a pelagic existence, probably rested on the bottom on their comparatively short arms. Indeed, it is probable, as is shown elsewhere, that these forms crawled about a good share of the time, rather than swam about freely.

It is a debatable question whether *Uintacrinus* was as gregarious in its habits as has generally been conceded hitherto. At the present day, it is true, *Antedon* swims about in schools, and *Actinometra* seems to be equally gregarious so far as observations have been made. In the past, *Agassizocrinus* seems to have lived together in great numbers, and the same was true of *Saccocoma*. These forms, however, I do not consider essentially pelagic as I do *Marsupites* and *Uintacrinus*. In European deposits *Uintacrinus* has been found as isolated specimens only. It is when we come to the Niobrara of Kansas that we have to deal with the curious "colonies" of *Uintacrinus*. Springer believes, as do all other writers on the subject, that *Uintacrinus* was gregarious in habit. He says on page 11, "These

crinoids were in detached masses, clinging together and floating in the open sea, entirely separate from other objects. They were actually swarming, very much like a swarm of bees when they leave the hive and settle upon some object—some on the outside and some buried underneath their fellows—all in the utmost confusion.

A. H. Clark (1909*a*, p. 129) devotes some attention to the ecology of *Uintacrinus*, although he suggests nothing essentially new. In one paragraph he arraigns authors as not having the "courage of their convictions" in considering *Uintacrinus* as a pelagic type, as shown by their figuring specimens with the mouth up. I think it has been generally conceded that *Uintacrinus* floated with the arms dependent. Indeed this is so obvious that no one has taken the trouble to point it out hitherto. The figuring of *Uintacrinus* mouth up is not such an evidence of weak faith as it seems to Clark, after all. This is the conventional manner of illustrating crinoids, and is followed out even in the case of the Calceocrinidæ by Bather (1893). A plate of *Uintacrinus* figures with the apical portions up would have to be reversed by the average mortal before becoming intelligible. Clark likewise gives some interesting views relative to the feeding habits of *Uintacrinus*. He considers that—

> the closer the individuals lived, the more advantageous it would be for them; for their food probably consisted of minute pelagic organisms which they intercepted with their long feathery arms; these organisms are largely lucifugous, and would tend to collect under the shadow of a mass of crinoids as they are known to do under floating logs and driftwood which, thereby, would be placed in the economically advantageous attitude of attracting to itself without effort its own food supply. The perisome of *Uintacrinus* is black, of such a dense carbonaceous black that it has been preserved without change through the ages which have elapsed since cretaceous times; and, if one of these small lucifugous organisms took refuge under the shadow of a mass of *Uintacrinus*, it would be quite likely to be attracted to the blackest portion of the animals, the disk or ambulacra, whereupon it would soon find its way (or rather be conducted) to the mouth.

Just why the disk is held to be black in the case of the living crinoids it is difficult to say. As described by Springer (1901) the tegmen is black, as carbonized animal tissues are apt to be. It has not hitherto been held as remarkable that carbonized matter should retain its blackness. Furthermore, the advantage of having the food attracted to the disk is not immediately obvious. The hundreds of pinnules borne on the arms are supposed to function as food-gathering organs, and they would not be specially benefited by a black spot an inch or so in diameter, several feet away.

It is inconceivable that the animals could have lived under such crowded conditions as has been predicated by the authors just quoted. For what purpose were the extremely long arms and other very special modifications other than that the animal might have the utmost freedom of movement? Again, how could any but a favored few, and even those in but a very insufficient way, obtain nourishment?

It is probable indeed that this "swarming" was the actual cause of the death of the crinoids, as has been suggested as a possibility by Springer. Setting aside the theory that the crinoids lived in more or less agglomerated masses it seems scarcely possible that they could have lived in freely swimming schools, as do the living Comatulæ. Arguing against the living of any considerable number of *Uintacrinus* in juxtaposition, one needs but to consider their great size. An adult fully expanded would cover an area of 30 or more square feet. Allowing for a reasonable amount of clear water on all sides, say a couple of feet, we would have the individual's space requirements greatly increased. Under these conditions it seems as if it would prove inexpedient for any considerable number of individuals to travel together.

There seems but one plausible explanation to account for the "swarming" of *Uintacrinus* and that has been put forward by Springer. He says: "It is possible that this may have happened during periods of sexual activity." We can easily conceive, under such conditions, of large numbers of *Uintacrinus* gathering together in favorable localities, such as bays or lagoons. Here possibly through the crowding of females about the males[1] a large number of individuals might become inextricably tangled together. Under such circumstances the individuals constituting the core of the mass must inevitably die of suffocation and starvation, though probably the former course may be held as the more efficient inasmuch as the whole incident could have occupied but a short time. Some of the individuals on the outer surface of the mass might be able to clear themselves by a breaking off of their arms, but the majority would be killed. Subsequent to the death of the animals the mass would sink to the bottom, and there form such lenses as we find to-day. On this hypothesis one may understand the absence of isolated specimens in this region. The crinoids came into the shallow waters during periods of sexual activity and afterwards returned to their normal habitat, perhaps far out in the open sea, leaving behind only an occasional mass of their unfortunate fellows.

A glance at a paleogeographic map of the Niobrara sea gives considerable support to the foregoing conclusions. The ancient Gulf of Mexico occupied in a general way the area it now covers, although it was considerably greater in extent. Passing northward into Kansas, however, was a great embayment. In the Gulf itself there was probably a strong Gulf stream much as at the present time. Out in this current, and probably farther out at sea also, the *Uintacrinus* spent the greater part of the year. In the breeding season they entered the

[1] The preponderance of females over males seems to be quite marked in recent forms. Among nearly thirty specimens of *Actinometra japonica* collected at a single locality at one time, there were no males. The females in all cases bore large numbers of nearly ripe ova. At the same locality *Antedon macrodiscus* likewise showed a very marked preponderance of females over males.

comparatively quiet waters of the bays in great numbers, and here, as before described, many lost their lives. The original locality where *Uintacrinus* was found, in the Uinta Mountains of northern Utah, represents another great bay. In both cases it is interesting to note that the crinoids are found in the innermost portions of the embayments where one would scarcely expect to find the conditions for which *Uintacrinus* is so obviously fitted. That the water was very shallow in which the beds containing *Uintacrinus* were deposited is generally conceded.

Another possible explanation of the formation of these masses is a variant of the foregoing. It may be when gathered in these embayments in the breeding season, that the crinoids were thrown together as a result of wind activity. They may even have been driven into the shallows and there been massed and stranded. The agitated chalk sediment of the bottom would quickly cover and serve to preserve the crinoids. Of the two explanations the former seems the more reasonable, inasmuch as the crinoids are as a rule most beautifully preserved and do not show the effects of violent disturbance.

The whole structure of *Uintacrinus* as noted above argues against a littoral habitat. The crinoid is evidently adapted only for life on the high seas, for elsewhere storms might well work havoc with the enormous but delicately constructed organism. The widespread occurrence of the genus again argues against a continuous shallow-water life. Living largely in the Gulf Stream, as they probably did, some followed the current and found a final resting place in the European Chalk. It seems possible that the type evolved in American waters, and here *Uintacrinus* chiefly flourished, a few straggling forms only making their way to the European seas. It is possible, of course, that in Europe the scarcity of the organism is due to the fact that as yet no breeding locality has been found, and that some day masses of *Uintacrinus* similar to those found in America will be discovered in those regions.

A. H. Clark (1909*a*) gives quite a different version of the breeding habits of *Uintacrinus* than that here suggested. According to him the eggs were laid and fertilized while the animals were moving about in the open sea. His idea can best perhaps be expressed in his own words:

> Now a floating colony of *Uintacrinus* during a breeding period would be drifted about, as at other times, by the surface currents, the waves, and the wind, just as the medusæ are; and, consequently, their embryos would fall over a large extent of territory. By the time the larvæ from such embryos as happened to fall upon suitable bottom had begun to grow, the parent colony would have drifted to a very considerable distance, unless, of course, the species was an inhabitant of inclosed bays, which, however, taking into account its enormous range, is quite unlikely; by the time the young were ready to discard their stems and swim away, forming a swarm of their own, the parent colony would be in some remote part of the sea. As the position of the parent colony

over any given area of sea bottom would not be of long duration, the young from the embryos which happened to fall at any given place would naturally be all of approximately the same age, and hence of the same size.

This casual peppering of eggs seems opposed to all that we know of the habits of the Crinoidea, and would furthermore be highly detrimental to the best interests of the organisms. In the first place, fertilization would by no means be assured, and, in the second place, the chances are that the majority of the eggs would fall in an unfavorable environment.

Such an hypothesis fails to explain the colonies of young individuals as it is supposed to do. Were the adult colony to stop at a given spot and discharge a large number of eggs, and subsequently were the eggs to develop and furnish young that acquired freedom at the same time and were imbued with the colonial habit, one might perhaps concede that this explanation explains the conditions as we find them. There are too many difficulties in the way, however.

On the other hand, the swarming of the crinoids in the breeding season certainly forms a plausible solution of the problem. One would expect crinoids of the same age to interbreed, and so we should expect to find any given colony composed of individuals of approximately the same size. There should be at least two or three distinct grades. The first would consist of year-old animals perhaps. The next year the crinoids might be of sufficient size to herd with the adults, although there may be a second-year group as well. A comparison of the size of individuals in different colonies might be used as an approximate index of the rate of growth of the animals.

As to the life history of *Uintacrinus* one can not be certain. It is probable that the eggs were laid in shallow, comparatively current-free water. Here they hatched and the larvæ become attached to the bottom. There seems no question but that a stalked stage was had, although, as will be noted below, exception has been taken to this view. Upon becoming detached from its column the young *Uintacrinus* probably remained in the shallow water of the embayment. It is probable that the first year at least was passed here, the animal not having sufficient swimming powers to reach the open sea. Such embayments could have but feeble currents, and the animals, in order to get from place to place, must have had to rely to a considerable extent on their own activity.

Clark, in the passage quoted above, speaks of the young *Uintacrinus* as discarding their stems. In a paper published at approximately the same time as the one quoted he has this to say: "The crinoids are the only recent fixed echinoderms; but in the fossil crinoids, as Lang pointed out in *Marsupites*, and I independently showed in *Uintacrinus*, there are forms which exhibit no evidence of having been attached; in fact the evidence is quite the other way.

In these forms the centrale may be instead of centro-dorsal really the dorso-central, in which case we should get an interesting homology with the echinoids."

Which paper has the precedence it is hard to say. It is quite evident, however, that in two papers, perhaps in press at the same moment, he reverses himself without in either case referring to the other paper.[1]

It is somewhat mystifying when and how Clark "independently showed" that *Uintacrinus* had never been attached. That *Uintacrinus* has no column, so far as known, has been established by the researches of Bather and Springer. The only way for Clark to prove the absence of a column, or its presence for that matter, is to trace the development of the form back until a stem is found, or back so far in the ontogeny of the animal that there is no chance of a column having been present. We shall await this proof with considerable interest.

The other two genera referable to Type II are of considerable interest, but they are so well known that any extended discussion of their structural features is scarcely warranted. There are, however, certain interesting structural deviations from those to be noted in the case of *Uintacrinus*. These deviations form an interesting example of adaptation to the same type of existence by crinoids belonging to fairly unrelated genetic lines. Any conclusions to which we may come relative to the derivation of these two genera are even more nebulous than in the case of *Uintacrinus*.

Marsupites.—In its adaptation to a free-swimming existence *Marsupites* (Pl. 10, fig. 4) differs from *Uintacrinus* in many important regards. The arms are comparatively short and bifurcate many times. The dorsal cup is large, but its size is due simply to the great size of the three circlets of plates and of the centrale. There are no interbrachials, and there is no incorporation of the proximal pinnules in the cup. The tegmen is composed of rather heavy plates, indicating the comparatively recent acquisition of a free-swimming existence.

In regard to this form Bell (1891, p. 210, footnote) has written: "I suppose no morphologist will be bold enough to say whether *Marsupites* or the irregular Blastoids are primarily or secondarily free forms." This seems to be the stand taken by A. H. Clark, at least in regard to *Marsupites*, as elsewhere quoted. It seems to me, rather, that it would be a bold morphologist indeed who has the courage to claim a primary free condition for these forms. Freedom is too easily secured, and symmetry is far too difficult to acquire to warrant such statements.

[1] Since writing the above I have been informed by Mr. Clark verbally that he believes *Uintacrinus* never to have been attached by a column.

Saccocoma.—Saccocoma (Pl. 10, figs. 1–3) is chiefly interesting because of its high degree of specialization. This form has well been described by Jaekel (1893). In this form the centrale is minute and may consist either of a new element to which the basals have been fused, or it may consist simply of the fused basals. The minute size of this plate compared with the size of the cup is surprising, inasmuch as in *Marsupites*, the other form the cup of which consists of but few plates, the centrale has been so considerably enlarged. The arms of *Saccocoma* are of great interest. Reference to the figure will show most unusual modifications. The arms are comparatively long and slender and in their distal portions are considerably branched. In their proximal portions the most noticeable feature is the lateral flange-like extensions of the arm ossicles. These are obviously adapted for use in swimming. The comb-like processes of the more distal ossicles probably represent modifications for a similar function. This small form, as has been held by Jaekel, probably swam about in enormous numbers in quiet lagoons. It is quite probable that as opposed to *Uintacrinus* this genus lived in schools as do the Comatulæ.

Abnormally free types—Carabocrinus.—Having discussed the members of Type II, mention should be made of those forms which subsequent to a complete loss of the column, evolve similar structures to those had by the three genera above described. This detachment from the column is unquestionably accidental in *Carabocrinus*, while in *Arachnocrinus* it seems that it may be a condition that becomes irregularly effective, though normal. These two genera are of very considerable interest as pointing to the probable derivation of the centrale. The case of *Carabocrinus* has already been described under the discussion of *Uintacrinus*. This is the most perfect example of the formation of a centrale where there is no possibility of the proximal columnal taking part in its formation. The evidence showing that this plate could not be other than an absolutely new skeletal element has already been given.

Arachnocrinus.—The genus *Arachnocrinus* offers us most remarkable and unexpected structures of a similar nature. The genus is an unusual dicyclic Inadunate which lived in the neighborhood of the coral reefs of the Onondaga seas. Apparently a column was possessed by this genus in the majority of cases, although the extraordinarily heavy arms could seemingly not be held other than as resulting from a special modification for an eleutherozoic habit. In the examination of a number of individuals of this genus in the course of the preparation of a memoir on the Devonian Crinoidea of New York State, I was astonished to find that no less than three individuals showed absolutely no trace of column attachment. In each of these specimens a centrale is to be observed. *Arachnocrinus* certainly had no proximale, and it seems evident that here again no other explanation

for its origin may be had other than that it represents an entirely new element. One of these crinoids is of special interest as showing a complete fusion between the centrale and certain of the infrabasals. This fusion quite parallels that to be found in the case of certain *Uintacrinus*.

One may only speculate as to the conditions under which an eleutherozoic habit was assumed by *Arachnocrinus*. It would appear that detachment from the column took place naturally but perhaps not universally. However such may be, we know that the form lived in the comparatively shallow waters about coral reefs where either an excessive shortening of the column or its complete elimination would tend to be induced. Subsequent to its acquisition of freedom it is probable that *Arachnocrinus* crawled about on the bottom rather than swam. The comparatively small size of the theca and the relatively enormous expanse of the massive arms seem to preclude the possibility of active swimming movements on the part of this organism. A full discussion of these remarkable crinoids will be given in a forthcoming work.

Having discussed the features more intimately associated with the different genera referred to this type, and having shown the presence of a centrale in certain normally attached forms, it may be well to recapitulate the evidence relative to the formation of this plate. This seems best as in the discussion of various types such facts have been scattered and used to illustrate specific structures.

Upon the loss of the column by a form in which a persistent proximal columnal is not present or in which specialization has not brought about a fusion of the proximal columnals into a centro-dorsal, we may have the formation within the proximal circlet of plates of an entirely new element. Subsequently this element may fuse with the adjacent plates of the cup, but this process is but a secondary one and of no great importance. In other cases, as will be pointed out later, upon the loss of the column the axial canal is closed simply by the increase in the size of the elements of the proximal circlet. This shows that the formation of a new plate is not essential. Furthermore it points to the possibility that in the case of *Saccocoma* we need not have had a centrale originally to which the basals fused. Instead the centrale in that form may represent simply the fused basals. At all events the centrale may not be held as of any considerable morphologic significance, and is of no great value in determining relationships.

It is unnecessary to enter upon a discussion of the homologies of the centrale, inasmuch as being an absolutely new element, it is not homologous with any structures in other crinoids. It may be seen that a consideration of it as representing the "dorso-central" or the

entire column of the Crinoidea is quite groundless. Nor may the centrale be compared with the apical plate of the Echinoidea, thereby giving a footing to far-fetched theories of mutual interrelationships.

TYPE 3.

Agassizocrinus.—The sole genus referable to this division is *Agassizocrinus,* which flourished in enormous numbers in the late Mississippian seas. The structure characteristic of this group is the close union and subsequent fusion of the proximal circlet of plates. No centrale was formed, apparently. As elsewhere noted *Saccocoma* may possibly belong in this division, for in that genus the "centrale" may simply represent the fused basals.

The infrabasals in *Agassizocrinus* are large and massive, while the axial canal is comparatively small. Upon detachment from the column a filling of the axial canal probably took place, but the resultant plug must of necessity have been insignificant in size, and may indeed never have reached the surface. At any rate no trace of the plug can be seen externally. A very close union was effected between the infrabasals, and in the majority of cases complete fusion took place in the adult stages. As a rule the fusion of the plates was followed by a secondary deposition of stereom over the entire surface of the infrabasal knob, which effectually obliterates all traces of sutures. In the figure here given (Pl. 10, fig. 5), it is to be noted that the infrabasal sutures are indicated. This is somewhat unusual for the genus. These fused infrabasals are preserved to us in great numbers, certain beds being largely composed of them associated with disarticulated calycal plates.

Agassizocrinus is particularly interesting because of the fact that the acquisition of an eleutherozoic habit is a comparatively new thing, and occurs in a line where such disruption indicates a wide deviation from the normal. In spite of this fact the innovation seems to have been a most successful one, judging from the prolific development of the genus. *Agassizocrinus* appears to have been near the termination of its genetic line, and it is perhaps on this account alone that it has not given rise to a line of eleutherozoic descendants.

As to the habits of *Agassizocrinus* little may positively be said. It seems highly probable that an eleutherozoic existence was maintained from a very early ontogenetic stage, for no trace of a stem cicatrix is to be seen. Considering the very heavy nature of the cup plates and the comparatively massive and short arms it scarcely is to be held that the animal was a free-swimming organism. Rather, I think it should be considered that *Agassizocrinus* for the greater part of the time crawled about on the bottom and was capable of swimming but short distances.

Scytalocrinus.—In connection with the discussion of *Agassizocrinus* should be noted a specimen of *Scytalocrinus* which abnormally exhibits similar structural features to those shown by *Agassizocrinus*. In this specimen the column has been completely lost. Although disruption from the column in this instance may be held to be abnormal, it may well represent the effect of a tendency toward an eleutherozoic habit becoming irregularly effective in this genetic line. *Agassizocrinus* is closely related to *Scytalocrinus* and a condition so universally assumed and maintained by this genus might well appear sporadically elsewhere among related types.

The specimen illustrating this unusual and interesting structure has been described in Troost's recently published manuscript (1909, p. 88) as *Scytalocrinus* (?) *gracilis*. Troost observed that the stem is wanting and that there seems to be no evidence of stem attachment. He therefore referred the specimen to the genus *Agassizocrinus*. Miss Wood, in editing the manuscript, referred the species to *Scytalocrinus*, a genus to which it may well be referred.

In this specimen there is no sign of fusion among the infrabasals nor has a centrale been formed to plug up the axial canal. The closing of this canal has been effected by a growth and close union of the infrabasals themselves. The crinoid probably did not lose its stem when young as Miss Wood supposes. A very definite flattening of the infrabasals marks the former stem cicatrix, and while there has been more or less resorption and solution there is every reason to believe that the column had reached a fair size before the crinoid became detached.

The anal side of the crinoid is badly weathered, and it is somewhat difficult to make out the true nature of the plates. Miss Wood in her notes has pointed out that one of the infrabasals seems smaller than the others and apparently does not reach the center. The infrabasals were undoubtedly nearly equal in size, but owing to weathering one has been nearly eliminated. This shows how difficult it is to judge accurately of the relationship of the other plates on this side. The plates certainly are not "much distorted." The left posterior radial seems abnormally small, and it is possible that the left posterior arm was partially aborted. Not enough remains now to be sure of this, however. The anal interradius seems fairly normal. The primibrachs of the left antero-lateral and right postero-lateral rays are curiously flattened on the sides toward the anal interradius, but this I attribute to weathering.

Miss Wood has suggested that the crinoid lay flat on the bottom. This explanation might well account for the apparent distortion and abortion of the plates and arms of the anal side, but is so opposed to the habits of the Crinoidea that one hesitates to accept it. The conditions as we have them may be accounted for on the basis of

excessive weathering, and such being the case it seems perhaps preferable to explain them on that basis. One would think that the development of the arms of this form is quite sufficient to enable the crinoid to use them as swimming or ambulatory organs and so obviate the necessity of maintaining a purely passive existence.

TYPE 4.

This group has been erected for the reception of two blastoid genera, *Eleutherocrinus* and *Zygocrinus*, and two cystid genera, *Protocrinus* and *Lichenoides*. This division obviously contains a rather heterogeneous collection of Pelmatozoa, all of which, however, have a similar arrangement of proximal plates as regards the closing of the apical aperture. In each of these genera the axial canal is closed by an increase in the size of the plates composing the proximal circlet, which become closely united but not fused. In this they agree with *Scytalocrinus*, described above, and with certain *Agassizocrinus* in which fusion of the infrabasals has not become effective.

Lichenoides.—Lichenoides, which has been described and figured by Barrande (1887) as well as the preservation of the material permits, must have lost its column at a very early stage in its development. As will be seen by reference to Plate 11, figure 11, the proximal circlet of plates is somewhat disarranged, and by a mutual adjustment of the elements the apical opening is closed.

Bather (1900) holds that the theca is "composed of rounded plates of very different size, but semiregular in arrangement. At the base are five to twelve minute plates." It seems to me that the cup is composed of four circlets of plates, with five plates in each range, as in *Macrocystella*, to which this genus appears to be closely related. The apparent irregularity of arrangement is due to a shifting of the plates subsequent to detachment from the column.

The systematic position of this genus is highly problematic. As stated under the discussion of *Macrocystella* above, the forms seem more closely related to the Crinoidea than the Cystidea, and might well be styled "tricyclic" Crinoidea. At all events one finds considerable difficulty in assigning them to the Cystidea.

Protocrinus.—In the genus *Protocrinus* (Pl. 11, figs. 12 and 13) it may be seen that attachment by a column was had until comparatively late in the life of the animal—at least in certain individuals. The specimen given as figure 12 apparently has four plates in the proximal circlet, and there is a well-defined stem-cicatrix. By the well-defined nature of the latter, it is evident that the column was comparatively well differentiated. In figure 13 all traces of stem attachment have disappeared. There has likewise been a fusion between two of the elements of the proximal circlet.

It is probable that in both this and in the preceding forms locomotion was effected by the animals crawling on the bottom. The appendages seem scarcely to be of sufficient size and strength to warrant the conclusion that they could function as efficient swimming organs unless aided by a considerable buoyancy of the theca, which in these cases seems to be wanting.

Eleutherocrinus and *Zygocrinus* differ from most other eleutherozoic Pelmatozoa either in not being essentially free-swimming organisms or in not crawling along the bottom with the theca raised above the surface. In their manner of life they simulate the Echinoidea among the Eleutherozoa and the Anomalocystidæ among the Pelmatozoa. A free-swimming existence was denied them, indeed, by the lack of proper organs of propulsion. Their slender, comparatively weak pinnules, ranged along the ambulacral areas, were incapable of the sweeping oar-like movements of the long stout crinoid arms. They could do creditable service, however, in pushing the crinoid along the bottom,

Eleutherocrinus.—Eleutherocrinus (Pl. 10, figs. 6–8) was descended from an essentially *Pentremitidea*-like ancestor. When the blastoid became detached from its column, it naturally lay lengthwise. Two points determined the side which was to lay next the bottom. In the first place the anal opening had to be on the lower side to prevent the excrement from fouling the spiracles and ambulacra. In the second place, as many of the ambulacra were to retain their unimpaired efficiency as possible. There are three possible positions meeting the first requirement; upon the right posterior ambulacrum, the left posterior ambulacrum, and upon the posterior interradius. In order to meet the second requirement, however, the posterior interradius must be eliminated from consideration. With the blastoid resting upon it, two ambulacra would have been rendered practically useless. Of the two positions left, the one with the left posterior ambulacrum resting on the bottom was assumed.

In motion the blastoid—not *Eleutherocrinus* as yet—progressed backward, as it were. That is, the apical portion formed the forward end. The reasons for this are obvious. If motion were to take place in the opposite direction, the sediment of the bottom would be pushed up over the oral openings. Moreover, the efficiency of the pinnules would probably be lessened.

The modifications in the structure of the blastoid as a result of the assumption of this type of existence are marked, and offer a beautiful instance of adaptation. The aboral end of the theca became sharply pointed, rounding above and flattened below. The left posterior ambulacrum became greatly shortened and widened, coming to lie entirely in the plane of the oral face. Thus we have the

lower portion of the body forming a smooth flattened surface, admirably adapted to sliding along the bottom.

Zygocrinus.—In *Zygocrinus*, from the Carboniferous of England, modifications apparently quite at variance with those to be observed in the case of *Eleutherocrinus* are to be noted. It is difficult in the extreme without an examination of original material to determine the nature and extent of these differences. It would seem, however, in *Zygocrinus*, that upon detachment the animal did not rest lengthwise upon the bottom, but upon the apical portion of the theca. If this be the case it seems highly probable that the ancestral type was subglobose as to form, and perhaps not unlike *Granatocrinus*. Motion in this curious genus seems to have been directed with the aborted ray forward. The genus is certainly a highly specialized and divergent type and if it bears movable spines as described the resemblance to the Echinoidea is considerably enhanced.

General discussion of Group II.—In the members of Group II it is to be noted that the greater portion of the column is lost and in certain cases no remnant of it remains subsequent to detachment. Maintaining an eleutherozoic existence, permanent refixation by cementation has in no case been observed. The loss of the column is even more remarkable than the assumption of a detached existence. The column is a highly differentiated organ and was only acquired after a long period of fixation. That such a highly specialized organ should suddenly be dispensed with is an interesting commentary on the way in which animals discard structures when it is to their advantage to do so. The wide assumption of an eleutherozoic type of life among such extremely variable organisms throughout geologic time further emphasizes the remarkable tendency there has been noted toward the assumption of freedom by the Pelmatozoa.

Group III.

The members of Group III as heretofore defined constitute those Crinoidea that do not possess a true jointed column but as a rule are cemented to the bottom by a base of varying composition. This base for purposes of convenience I have styled a peduncle. The bearing that these pedunculate forms have on eleutherozoic conditions as they obtain among the Pelmatozoa may not be immediately obvious. It seems highly probable, however, that these forms represent an effort on the part of the Crinoidea to assume a detached existence, a tendency that has become but partially effective. Furthermore, in one genus at least to which we shall devote most of our attention both an attached and detached existence is maintained, even within a single species. At all events the cause for the assumption of such structures as are possessed by the members of this group

is doubtless of very similar nature to those that have brought about an eleutherozoic habit on the part of other crinoids. It is for this reason that these forms have been introduced in the present paper.

Edriocrinus.—The genus *Edriocrinus* has long been known, although its genetic affinities are but poorly understood. It has a fairly long geologic range, being found from the New Scotland to the Onondaga. Its structure is apparently very simple, as will be seen by reference to Plate 11, figures 1, 2, 9, 14, 15. The cup consists of five radials and an anal plate. The latter is somewhat narrower than the radials but of equal height. This cup rests upon an apparently amorphous base. The arms are short but remarkably broad and stout, indicating adaptation perhaps more to a shallow water habit than to an eleutherozoic existence. The shape of the base and the relation of the thecal plates to it vary considerably. This variation is immediately obvious in a comparison of Plate 11, figures 1 and 9.

Edriocrinus dispansus, new species (Pl. 11, figs. 1 and 2), offers perhaps the most interesting variant from the normal *Edriocrinus* structure. In this species, which occurs in the Linden (Helderbergian) of Big Sandy River, Benton County, Tennessee, the base is greatly expanded. In the specimen here figured the animal is attached to a shell of *Leptæna rhomboidalis,* which it entirely covers and extends beyond. Despite the great expanse of the lower portion of the cup, the diameter of the theca at the arm bases is comparatively small. It is to be noted that the radials and anal are directed inward, rather than vertically or outward, as in the case of most Crinoidea. As a result the radials are considerably broader at the base than at the top. There is no other species of *Edriocrinus* that in any way approaches this form. The holotype of this species is in the United States National Museum. (Cat. No. 27757.)

As going to the opposite extreme from *Edriocrinus dispansus* should be taken *E. pyriformis.* In this species (Pl. 11, fig. 9) the peduncle is comparatively slender and elongate, having more the appearance of a short, fairly stout column. The other species of *Edriocrinus* lie intermediate between this and the preceding species, both structurally and geologically.

Edriocrinus sacculus, from the Oriskany, is a type that offers many interesting features relative to the structure of the genus. It is through the evidence of this form, for instance, that we know anything in regard to the structure of the arms of *Edriocrinus.* This species likewise combines an eleutherozoic and statozoic habit. The species is constantly attached in the young forms, as may be noted in Plate 11, figure 14. The young apparently were often associated in groups or clusters as here indicated. A number of these clusters have been noted where the young are cemented to brachiopod or gastropod shells. In certain individuals it appears that attachment was main-

tained throughout life. In the majority of cases, however, detachment from the bottom took place. Detachment became effective through the resorption of the stalk near its base. This resulted in the freedom of the organism. Detachment in the case of these crinoids apparently occurred at widely different periods in the development of the animals, for attached forms of widely different sizes may be observed. Figure 14, Plate 11, probably represents the approximate size at which detachment normally occurs, for the majority of attached individuals seem to be of about this size or smaller.

Subsequent to detachment *Edriocrinus* perhaps moved from place to place by crawling on its stout arms. The position assumed by the specimen of *E. sacculus* as given on Plate 11, figure 15, is probably the natural one. As here shown *Edriocrinus* is crawling over the surface of a large gastropod. It does not seem possible with the comparatively feeble musculature of this genus and the stout arms that are borne that the animal could have been capable of very effective swimming movements.

The origin of the peduncle as possessed by *Edriocrinus* may not certainly be determined. It seems probable, however, that it consists in part at least of fused columnals. Early in the ontogeny of the animal it may well be that the crinoid became detached from its embryonic stem and swam about freely with but a few columnals attached to the theca. Instead of thereafter maintaining a detached existence the crinoid settled down and became cemented to some object on the bottom. Subsequently a coalescence of the constituent columnals took place, resulting in the formation of such structures as we find.

Edriocrinus has been placed among the Flexibilia largely from the want of a better place to put it. Its apparent lack of pinnules has caused it to be grouped with the Impinnata. It does not seem evident that this grouping is correct, for the genus does not behave as one would expect a member of the Flexibilia to do. The evidence of the lack of pinnules is highly inconclusive. Indeed I think that the use of this character in classification must be attended with considerable caution. There has probably never been a crinoid which might truly be styled impinnate. The pinnulæ may be more in the nature of tentacles perhaps and need not be strengthened by calcified ossicles but they are nevertheless pinnulæ. Upon occasion centers of calcification may appear within these pinnules and ossicles be formed. Even with the formation of definite ossicles it does not necessarily follow that the pinnules would be preserved to us to-day unless there be a very close union between the constituent ossicles and between the pinnulæ and the arm proper. Bather argues for the origin of pinnules from bifurcation of the arm, but I hold that

in all probability the opposite process has obtained. At times, no doubt, arm branches have become reduced in size forming ramules and even ultimately what might be styled pinnules. However, I do not think that this has been the normal process.

As has been elsewhere noted, certain fossil Crinoidea may be held to have led an epi-planktonic existence, being attached to floating wood. *Edriocrinus* may be added to the list of epi-planktonic types. The species involved is probably *E. dispansus*, a fairly young specimen of which has been found attached to the float of a *Scyphocrinus*. The *Edriocrinus* was cemented to the lower surface of the bulb, and inasmuch as these floats are almost invariably found in the rocks with the lower surface down, it seems probable that attachment was had while the *Scyphocrinus* was alive and freely floating.

Cotylederma, Eudesicrinus, and *Holopus.*—For comparison with *Edriocrinus* figures are here given of the curious genera *Cotylederma, Eudesicrinus,* and *Holopus* (Pl. 11, figs. 3–5, 6–8, 10). It will be noted in all of these forms that the crinoid is cemented to the bottom by a solid calcerous disk. No infrabasals or basals are to be observed. The origin of these forms, as in the case of *Edriocrinus,* is more or less obscure. Likewise the composition of the base by which the crinoid is cemented is a matter of conjecture. It is only I think by tracing the possible derivation of these crinoids that we may get a clue as to the composition of the peduncle. It is not essential in tracing the evolution of these forms that we establish the exact genetic lines. Rather we should attempt to establish the evolution of the structural features that might evolve such a type of base.

Origin of pedunculate type of structure.—The evolution of these forms may perhaps be held to be somewhat as follows: Having a stalked ancestor with a well differentiated proximale, detachment becomes effective immediately beneath this plate. For a time a free-swimming or possibly crawling existence is maintained. Subsequently reattachment takes place. This is accomplished by the cementation of the proximale to some object on the sea bottom. If such be held to be the origin of the peduncle we may consider it to have essentially the composition of a centro-dorsal, barring the lack of cirri.

The reason for refixation in these forms is not altogether clear. As is elsewhere noted there is considerable evidence to prove that alternate periods of freedom and fixation frequently obtain among the Pelmatozoa. In these genera this condition may be expressed in a single period of freedom followed by permanent fixation throughout the subsequent life of the organism. The reason for the lack of maintenance of an eleutherozoic habit may not certainly be stated although there are several possible causes. It may be that the structure of the arms in these genera is not such as to enable them to

function as efficient ambulatory or swimming appendages. There are so many factors indeed that might influence the crinoids that there is small choice between them. The important fact after all is that cementation did take place.

Jaekel (1891) has combined these genera with the Eugeniacrinidæ, near which they unquestionably belong. It seems probable furthermore that different though closely related genetic lines may be represented. A tendency becoming effective in one line would be bound to crop out among other related types.

CONCLUSIONS.

In the preceding portion of this paper an attempt has been made rather toward the enumeration of specific instances of detachment of the Pelmatozoa and the consequent modifications as shown by certain types than toward the broader features as influencing the class as a whole. It may be well to bring together the more pertinent facts relative to the assumption of an eleutherozoic habit among the Pelmatozoa indicating in a broad way the general tendencies to be observed. This will of necessity include a comparative study of the manifestations of an eleutherozoic habit as shown in the various groups and by the different classes of the Pelmatozoa. The probable proximal causes for the assumption of this mode of life will also be treated in a general way. It was originally intended to discuss at length the influence of the widespread acquisition of freedom on the symmetry and distribution of the Pelmatozoa, but such topics though germane to the subject matter of the present paper may perhaps best be treated independently in separate articles.

A review of the evidence relative to the maintenance of an eleutherozoic habit among the Pelmatozoa will show that such a form of life has widely been assumed and maintained among the Cystidea, Blastoidea, and Crinoidea throughout their history. In each class highly specialized types have been evolved, the degree and nature of the specialization being dependent in the main on the structure of the organisms involved. Among the stalked, erect forms detachment from the bottom may be held as an almost universal attribute. At times the period of detachment may be brief and succeeded by a period of fixation. Again, there may be several alternating periods of attachment and freedom. Such may be held to be the normal mode of life of the majority of the stalked Pelmatozoa.

It is obvious, I think, that those forms among which a detached existence is largely maintained are to be derived from types whose periods of freedom were of short duration. Whether there ever existed a stalked Pelmatozoan that was sedentary from the time of its attachment is a question that must unfortunately be forever open. One might argue that such should of necessity be the case in order to

account for the radial symmetry of the Pelmatozoa. According to the hypothesis of A. H. Clark, which will be discussed at length at some future time, the acquisition of radial symmetry is in no wise dependent upon the type of life led by the ancestral forms. Radial symmetry, according to his views, may be evolved equally as well in eleutherozoic as in statozoic stock. It is impossible to completely accept these views, but it does seem probable that absolute fixation throughout the life of the individual for many generations is not essential.

We may assume that from the very primitive eleutherozoic echinoderm stock there split off a group in which a statozoic condition of life was the prevailing tendency. Within this general stock there probably were strains in which this tendency was more deeply impressed than in others. Be this as it may it seems likely that in the history of the Pelmatozoa there was a period in which a statozoic habit was the prevailing and dominant character. This period lies intermediate between that in which freedom is the expression of nonspecialization, and that in which an eleutherozoic existence is the expression of a still higher degree of specialization among types of considerable complexity. It is no doubt largely to this intermediate stage that the Pelmatozoa owe the indelible impress of a statozoic existence as evidenced by orthogenetic tendencies made manifest even to the present day.

Among the Cystidea we find the only eleutherozoic Pelmatozoa that may not be held as having descended from a long line of statozoic ancestors. Even in this class there are but a few of the many-plated types that may be claimed as having evolved from a stock in which fixation had not become effective. These many-plated Cystidea were short-lived and never of commanding importance. With but one exception indeed there seems to have been no line which persisted for any considerable length of time but that was derived from a stock in which a statozoic habit had been deeply ingrained. The exception is that of the Anomalocystidæ, where it would seem that an eleutherozoic habit had been early assumed and constantly maintained. It is probable, however, that even in this line descent was had from Cystidea among which fixation at least became irregularly effective.

Causes for assumption of detached existence.—When the general tendency among the Pelmatozoa seems, superficially at least, to be constantly toward the perfection of organs for purposes of attachment, it is difficult to see the reason for such widespread departure from statozoic conditions. The assumption of an eleutherozoic habit may by no means be held as a reversion, but instead is to be considered as a well-defined progressive tendency. The causes of this deviation from the indicated path are not immediately obvious. It is probable

indeed that they are of two sorts, to a certain extent mutually interdependent. In the first place detachment may be forced upon the organisms by stress of physical conditions under which the animals live. In the second place it may be assumed as a character largely benefiting the race.

A discussion of these factors is of no small interest as showing to what extent the disruption of the column is optional and to what extent it is involuntary. There are two possible processes by which detachment may be attained among living Pelmatozoa. In the first place we may have a violent disruption of the column through the agency of some physical force. In the second place we may have voluntary detachment, following partial resorption of the column. Both of these processes have no doubt at times been effective.

Detachment by violent disruption.—In order to make valid the hypothesis of violent disruption of the crinoid column one must first have a physical agent competent to cause such a break. The only plausible explanation would be that of severe wave action. The assumption that crinoids may live at depths at which wave activity might act with considerable intensity is not wholly unwarranted. As has been elsewhere cited, *Isocrinus* has been reported at depths of approximately 20 fathoms. It is said, however, that they live in much shallower water than this even. After heavy storms the shores of certain coasts are said to be strewn with fragments of *Isocrinus*. Carpenter (1884, p. 289) records that after a gale *Isocrinus* of all ages and sizes were cast up on the shores at Barbados. This must indicate a very shallow water habit for *Isocrinus* at that locality. Certainly were we to find the modern representatives of the Crinoidea living at such extremely shallow depths as to be destroyed by wave action and cast up on the shore, we may equally well expect the Paleozoic forms to have lived in water shallow enough to subject them to considerable wave violence.

Involuntary detachment of the crinoids may have been a not uncommon, and consequently an important occurrence in Paleozoic times. As mentioned above, it seems possible that the sea bottom was quite within the range of wave action, at least in cases of violent storms. If this were true we may readily conceive of the crinoids being torn loose from their anchorage and leading an eleutherozoic existence for a time at least, while they were seeking favorable locations for reattachment. The beds of crinoid roots at Waldron may well be an instance of this sort. These were adult specimens and it seems highly improbable that the entire colony would break loose and migrate to another point voluntarily.

Such involuntary detachment may have been especially common in the case of young forms. It seems reasonable to expect that these may have lived in much shallower water than the adults. The case

of the Ordovician crinoids at Kirkfield, Ontario, seems to indicate such a condition of affairs. Here we have the bases of the crinoid columns cemented to an old, hardened and eroded sea bottom. It is obvious that this area had been emerged and upon its sinking the crinoids came in with the gradually advancing sea. The lack of sediment, and the fact that the crinoids are cemented directly to this eroded surface, indicate that the crinoids lived there very shortly after submergence. Submergence in such cases is admittedly a gradual process and of necessity these crinoids must have lived in quite shallow water. It is evident that even moderate wave activity would serve to loosen these crinoids from their points of attachment.

Effect of forcible detachment on the organisms.—It may easily be seen that if the majority of the Pelmatozoa were forcibly detached at different times in their ontogeny, and were they to live under such conditions that they might at any time be torn from the bottom, no complicated organs for the purpose of permanent fixation would tend to be evolved. Rather, the exigencies of such a life would tend to perfect the organism in the way of acquiring structures for temporary attachment, or to cause them totally to abandon all attempts toward permanent fixation. Here, with the exception of those Cystidea where fixation had not yet become wholly effective, we probably see the prime cause for the inception of detached conditions among the Pelmatozoa. Generalizing, one may say with a considerable degree of certainty that a free-swimming or pedunculate form of existence among the Crinoidea is induced by a comparatively shallow water habitat. Although free-swimming crinoids are found at great depths, it is only reasonable to suppose that they have secondarily sought the abyssal zone. The greater number of free-swimming crinoids are to be found either in shallow water or in regions largely affected by strong oceanic currents.

Having to a greater or less extent forcibly been compelled to assume a semidetached existence generation after generation, it is but natural that in certain lines a tendency would be induced toward the more perfect acquisition of such a mode of life as being of considerable benefit to the animals. Such a tendency is apt to make itself most evident among the terminal members of various genetic lines. Here, probably owing to the impaired force of the tendency toward fixation, complete detachment from the column may become effective. This freedom of the animal is further made possible by the possession of structures that are sufficiently perfected as organs of locomotion to enable the echinoderm to maintain a truly eleutherozoic existence.

Advantages of a detached existence.—The ability of a crinoid to move from place to place is obviously of great advantage. Irrespective of the movement of the ciliated larvæ, selective migration of the adults largely makes for the welfare of the Crinoidea. Granting that

such ability was possessed by many of the Crinoidea, as we may well be safe in assuming, there are a number of reasons for such migration. The most obvious reasons, perhaps, are those relating to the betterment of physical conditions and food supply. These two factors are more or less mutually dependent, naturally. In a sea lacking currents, and at approximately the same depth, with uniform conditions of sedimentation there would be little choice in location. Such uniform conditions seldom if ever obtain, however, except in comparatively restricted areas. The contour of the sea bottom, particularly in the shallow epicontinental seas, must have varied somewhat, making certain areas more suitable for the crinoids than others. Far more important, however, are the effects of currents, the presence of which in the Paleozoic seas may be assumed with a considerable degree of assurance. These currents would largely affect the food supply, and the Crinoidea if able to orient themselves in relation to such currents, might obtain optimum food conditions.

It is quite conceivable that the ciliated larvæ may not have settled at a locality entirely favorable to an adult crinoid. Indeed, the spot most suitable for the needs of the very young crinoid might well be far from desirable for the adult. Again, it is quite possible that during even the short life of a crinoid, conditions might so change as to make an originally favorable area less congenial. Moreover, in order to bring about a wider distribution of the Crinoidea, post-larval locomotion would be a factor of very great value. The importance of a wide distribution in contributing to the welfare of a group is at once apparent.

Bearing of detachment on distribution.—The distribution of the Crinoidea is necessarily effected by movement of the animals themselves. The change of location takes place either in the larval or the post-pentacrinoid stages of development. It has been considered hitherto that larval dispersal is the chief factor in controlling distribution. As indicated above we have a great deal of evidence going to prove that an eleutherozoic habit is largely maintained by the adult crinoids. It is here held that this post-larval freedom is of considerable importance in supplementing the activity of the meroplanktonic larvæ. The facts of crinoid distribution, and particularly of their segregation, argues strongly for considerable post-larval shifting among the Crinoidea. These topics, as elsewhere noted, will be discussed at length in a future paper.

Bearing of detachment on struggle for existence.—A prime reason for the maintenance and further perfection of eleutherozoic conditions not only among the Pelmatozoa, but among the Echinoderma in general, is in order to escape the intense struggle for existence that obtains in the crowded colonies of the bottom. The ciliated larvæ are probably of far less importance as effecting distribution among

the Echinoderms than is generally assumed, as is evidenced by the great numbers of pentacrinoid larvæ that are to be found in immediate proximity to the adults. Indeed, it has frequently been observed that these larvæ are attached to the arms and cirri of the mature crinoids.

Those types that have assumed a pelagic habit, such as *Uintacrinus* and *Marsupites* express the highest degree of specialization known among the Pelmatozoa, in search of easy conditions of existence. Among all the Echinoderma they may be noted as having most nearly reached optimum conditions of life, so far as the struggle for existence is concerned. As has been pointed out by Brooks (1899), pelagic life is the easiest of all types of existence. The life of such epi-plankton as *Pentacrinus* is far less favorable in that many individuals may cling to one bit of floating wood and thus materially cut one another's food supply.

Causes for reattachment of Pelmatozoa.—Despite the advantages of a detached mode of life we have considerable evidence showing that re-fixation frequently becomes effective subsequent to a period of freedom. Indeed, it seems highly probable that seldom if ever has a crinoid passed its entire life rooted to one spot. The reasons for the nonmaintenance of an eleutherozoic habit by many crinoids where disruption of the column has been caused by physical agency, is probably due in large part to the fact that in these organisms the tendency toward fixation is still a potent force. It must be remembered that even in the detached forms no great activity is maintained by the Crinoidea. Carpenter states that among the Comatulæ, for instance, the crinoids do not swim about actively except at the periods of reproduction. Again, it may well be that only those forms maintain an eleutherozoic type of existence which from their structure are capable of effecting a fair degree of movement. This may either be brought about through the acquisition of some buoyant structures or suitable modification of the arms to enable them to function as swimming or ambulatory appendages. In most cases it would seem that the nature of the arms is the determining factor as regards the maintenance of such an existence. Were crinoids to become detached that are but poorly equipped to live as eleutherozoic types, what is more natural than that they should again become affixed?

Evidences of the assumption of a detached existence.—Naturally, the most obvious indication of the maintenance of an eleutherozoic existence by a crinoid, is the lack of a column or pedicle. As has been shown above, however, a number of stalked forms were quite as free in their habits as some of the non-stalked. In such cases one generally finds a tapering stem, usually looped at the end and unprovided with roots or a terminal plate for attachment. A column provided

with cirri throughout the greater part of its length, especially if these be equipped with terminal claws, such as is shown on Plate 4, figure 2, is an equally good indication that the animal is free-swimming for a greater or less part of its existence. Among the prostrate Cystidea and Blastoidea, which crawled along the bottom, an eleutherozoic form of existence is clearly indicated by the marked modifications to be observed in the structure of the theca. These modifications have been discussed at length under such genera as *Eleutherocrinus, Pleurocystis,* and *Anomalocystis.*

Aside from such obvious signs of the maintenance of an eleutherozoic habit there are many more, the significance of which may only be appreciated when considered in the light of structures brought about through such a type of life. Inasmuch as semi-detached conditions so largely obtain among the Pelmatozoa, it is evident that throughout the Grade we have to deal with these modifications. It is only when organs become highly specialized and obviously adapted to eleutherozoic conditions that we feel safe in assigning such an origin to them, however.

The sporadic deviations and the earlier variations from the statozoic stock have characters more or less peculiar to themselves. It should be remembered that these types possessed no long ancestral lines that as Pelmatozoa had assumed a detached existence. As a result, there had come to be no special modifications fitting the forms for such an existence. These earlier types, therefore, are characterized by the absence of special organs such as cirri. Instead, it seems that they as a rule had not yet lost the semi-prehensile columns of their ancestors, and could upon occasion attach themselves by coiling the distal portion of their tapering columns about some stationary object.

Gradually, as an eleutherozoic existence was more universally assumed, and was perpetuated generation after generation, modifications of structure became manifest. Movement probably never was rapid or continuous for any prolonged period of time. As a result, in most forms we may look for but slight modification in the theca of the crinoid. Where modifications became most effective were in the arms and column.

Effect of a detached mode of life on the column.—The modifications which one would expect to find in the case of the column are of a twofold nature. In the first place the length of the column would be affected, and in the second structures capable of balancing and temporarily holding the animals would be perfected. As is well known, crinoid columns are prevailingly short—at times surprisingly so. To attribute this shortness of column to an eleutherozoic habit would be presumptous, for it is obviously incapable of demonstration. That such a type of life may have been of considerable importance in

bringing about conditions as we know them, or in *preventing* any considerable *increase* in the length of the columns, seems a reasonable supposition, however.

Bather (1900) believes that the assumption of a detached existence by the Pelmatozoa results in a marked abbreviation of the column, drawing this inference from the facts as we know them in the case of *Millericrinus prattii*. It is not evident that this case may be assumed to be typical. An eleutherozoic habit in the majority of cases probably did not result in a marked shortening of the column. Indeed, the longest columns reported are those of the fossil *Pentacrinus* which occurred in types which probably were not attached. The columns of crinoids have at no time been of great length, and it may well be that the widespread maintenance of an eleutherozoic habit as here assumed may have had much to do with keeping the columns within moderate bounds. It is probable only in special cases where other factors enter into the question that we have an appreciable abbreviation of the stems.

A fairly long column would be of considerable advantage to a crinoid whether free or attached. Of course in the case of complete separation of the crown from the column these advantages are more than compensated for by the additional degree of freedom. In the case of stalked forms however, a moderately long stem would serve as ballast either with or without a terminal weight and give the crinoid a certain degree of stability while at rest. The advantage of this is at once apparent. It is apparently necessary for crinoids at times to be stationary. The instances of comatulids dying in a bowl of water wherein there were no pebbles or other objects to which they might attach themselves is well known. Other specimens similarly placed but with objects to which they might attach placed in the bottom of the bowl live for some time. Again, moderately long columns would be of advantage as keeping the crinoids well above the sea bottom. The advantages of this are obvious both to the animals themselves and to the young of the colony. The impossibility of the young finding a foothold in a colony of well grown Comatulae has well been stated by Clark (1909, *a*).

The formation of prehensive cirri may directly be attributed to the maintenance of an eleutherozoic existence, however. Wherever found, there we may postulate free-living crinoids. It is evident that in the case of purely statozoic forms nothing could be more useless than appendages designed for holding to extraneous objects. In earlier times the cirri were comparatively simple, but so specialized have they since become that isolated cirri of certain *Pentacrinidæ* and comatulids can be distinguished with difficulty. Even the terminal claw has been developed in the stalked forms (Pl. 4, fig. 2). The function of these cirri has been primarily no doubt that of

temporarily anchoring the crinoid. It was suggested by de Loriol (1878, p. 12) that the cirri were used as organs of locomotion, a supposition that may in part be right, as is elsewhere indicated. The development of these cirri even in Paleozoic times is most noteworthy. For example, in *Cordylocrinus*, and particularly in a new Camerate genus from the Hamilton a most extraordinary development of cirri is to be noted. In some cases these cirri reach from well down on the column to considerably above the tips of the arms, the total length being two to three times the total height of the crown. In both of these genera, and particularly in *Cordylocrinus*, the crown is frequently so completely covered by cirri as scarcely to be visible. As has been noted under *Cordylocrinus*, the columns are remarkably short, measuring but a few inches in length, and show no signs of permanent fixation.

In connection with the formation of cirri as induced by an eleutherozoic habit should be recalled the grapnel of *Ancyrocrinus*, the float of *Scyphocrinus*, and the distal knobs of certain Devonian Camerata. The float of *Scyphocrinus* is unique and is a type of modification scarcely to be looked for. The distal excrescences, and the grapnel of *Ancyrocrinus* are obviously for the purpose of balancing the crinoids, as no doubt is the fused distal portion of the *Lepadocrinus* column.

It is a noteworthy fact that among the Crinoidea, especially in the later forms, the stem is frequently lost, or but a remnant of it remains. Among the Cystidea this is never the case. The reason for this is obvious. In the latter group the column has not become so highly differentiated an organ as among the Crinoidea and Blastoidea. It still contained a portion of the visceral mass, in all probability, and could not readily be shed. Again, the stem had not become so highly specialized for purposes of attachment that it could not be modified so as be made a useful adjunct in the propulsion of the animal.

Effect of a detached mode of life on the arms.—The tendency toward more perfect freedom—that is, toward directed movement—would of necessity find expression in a strengthening of the arms and their more perfect adaptation as swimming organs. Concomitant with such modification and induced by the mechanical influence of the arm-action may be noted a modification of the tegmen, both as to composition and orientation. These features are of indifferent value in many cases, no doubt, owing to the variable degree in which freedom was assumed, probably even within a closely circumscribed group. Under such circumstances the influence of a given type of life, held for short or variable periods, has to contend with cumulative tendencies induced by a diametrically opposed form of life held for the greater part of the lives of the common stock. Moreover,

there are opposed tendencies apparently inherent in the strain, such as the assumption of a heavily plated tegmen by the Camerata, the cause for which may be far to seek and which of necessity may never definitely be determined. The modifications of the arms proper which would be of value in an eleutherozoic existence are on the other hand not incompatible with their functions as organs of purely statazoic forms.

The brachial appendages of the Pelmatozoa subserve two vital functions—the gathering of food and the bearing of sperm or ova. Obviously, the greater the surface area exposed by the arms of a crinoid, the more perfectly will they fulfill their mission. In order adequately to extend this surface area, a musculature of sufficient strength and complexity to spread and close the rami is essential. The arm area is increased chiefly by bifurcation of the rami and by pinnules. Increase of arm area, unless carried to excess, as in certain *Actinometra*, is of positive value in locomotion, as offering a greater surface for catching the water. The modifications of the musculature to adapt it the more perfectly to function as a motor system would be simply an increase in the complexity of the system already possessed. So it may be assumed that while the modifications of the arms tend to be mutually strengthened, the tendencies in the modifications of the vault and theca in general may work at cross purposes in forms having variable statozoic and eleutherozoic ancestry.

Up to a certain limit, as before noted, an increase in the arm area of a crinoid would prove of advantage in perfecting these appendages as swimming organs. A similar result might be even more effectively brought about by the broadening of the rami themselves. Such broadening is to be noted in the genus *Eretmocrinus*, the remarkable paddle-shaped arms of which are so well known. A quite similar broadening of the rami is to be found in *Aorocrinus*, *Coelocrinus*, and *Dorycrinus*, although such structures have apparently not hitherto been noted in the case of these genera. This remarkable broadening of the rami may be explained on other grounds—as, for example, giving greater food-catching area. The same result could be more expeditiously and advantageously attained by a slight lengthening of the pinnulæ, or by bifurcation of the arms such as is common among closely related genera. The beautiful adaptation of these arms to swimming conditions is at once apparent, and it does not seem highly improbable that such was an important part of their functions. Again, we have the hooks on the pinnulæ of *Cactocrinus* (Pl. 5, figs. 4, 5) which hold the pinnulæ together much after the fashion in which the barbs of a feather are joined. So fastened together, the pinnulæ might well have offered a most effective surface for catching the water in swimming.

If we concede a general participation of the Crinoidea in an eleutherozoic existence, it will be well to bear the fact in mind, as affecting the type of arm-branching, the modification of articulations, and the general structure of the arms. We know, for instance, that in at least two species of *Mariacrinus* there is little or no ground for the supposition of an attached existence. May we not then legitimately wonder if the curious arm modifications of the Melocrinidæ, the atrophy of the outer and the hypertrophy and fusion of the inner rami, is not perhaps due to the assumption of an eleutherozoic existence by the stock? We may not expect identical or even similar modifications of arm-structure in different lines, for that is not the way of crinoids. We may expect, and we do find, if we look for them, modifications peculiar to the several lines, but all tending to the solution of the same problem. So it is with other crinoid structures.

Effect of an eleutherozoic existence on the symmetry of the Pelmatozoa.—The assumption of a completely detached form of life by certain Pelmatozoa gives one an excellent chance to study the effect of free movement upon a type whose radial symmetry has been impressed upon it by countless generations of statozoic ancestors. We have been assured by A. H. Clark (1909, p. 685) that radial symmetry does not depend upon a sessile ancestry. The octopus cited as an example to prove this assertion scarcely tends to confirm Clark's statement, however. The amount of modification resultant upon the change from a fixed to a free existence depends entirely upon the type of locomotion adopted. In the case of a crinoid, with its five equal rays, the changes in symmetry are not of great magnitude and probably were brought about but slowly. The exocyclic disks of *Uintacrinus* and *Actinometra* are perhaps directly to be attributed to a free-swimming life. As opposed to the for the most part freely swimming Crinoidea, we have to consider the crawling *Eleutherocrinus* and *Zygocrinus*. Here the changes, as pointed out in the discussion of the genera, are far reaching in their effect upon the structure of the animal. The amount of modification seems to vary directly as the amount of friction applied to the body of the animal while in motion. The body propelled by its appendages through a uniform medium, suffers little change, but given a drag on the body, as exacted by movement along the bottom, and we have results expressed in no uncertain terms. Naturally, to be effective, movement must take place in a given direction, as far as the orientation of the animal is concerned.

Effect of a detached mode of life on the distribution of the Pelmatozoa.—The almost universal assumption of freedom by the Pelmatozoa can not have other than a most marked effect upon the distribution of the

organisms. Even more important is the bearing such eleutherozoic conditions have on the minor movements of the animals, as evidenced by their segregation. It seems highly probable that the characteristic colonial habit assumed by the Pelmatozoa is due in large part to the selective migration of the echinoderms in their post-larval stages of development. This is a highly important topic and one that will be discussed at length in a subsequent paper.

Types of life led by the eleutherozoic Pelmatozoa.—A comparative study of eleutherozoic Pelmatozoa as regards their mode of life consequent upon the assumption of this form of existence is one of considerable interest. For purposes of convenience we may recognize three groups of eleutherozoic Pelmatozoa—those forms that constantly remain upon the bottom; those that are capable of swimming, but either temporarily attach themselves to the bottom or crawl; and, finally, those forms that are truly pelagic.

All of the stalked Pelmatozoa, with the exception of *Scyphocrinus* and certain *Pentacrinus*, may be held as vagile benthos. Among these benthos an erect position is almost universally maintained. The only known exceptions are to be found among the Cystidea as evidenced by such types as *Pleurocystis* and *Anomalocystis*. Among those forms where the stem has been entirely eliminated or but a few ossicles remain, movement is effected either by swimming or by crawling upon the bottom in an inverted position. Among the swimming types are to be found the most highly specialized eleutherozoic Crinoidea, such as *Uintacrinus*. These may be held as true plankton in their adult stages, inasmuch as they constantly maintain a pelagic existence by virtue of their own swimming movements.

It may safely be assumed that the stalked eleutherozoic Crinoidea spent but a small part of their time in motion. Having reached a favorable spot the natural tendency would be to remain there. It may be argued that under these conditions permanent fixation would become a necessity. This does not follow, however. In the case of cirriferous individuals temporary fixation is no doubt assumed by the clasping of some projection on the sea bottom with the cirri. Those forms with prehensile columns could loop the distal portion of the column about some stationary object. *Ancyrocrinus*, with its grapnel, might anchor almost anywhere. That even such types of fixation were unnecessary seems to be indicated by those columns above mentioned in which the distal extremity is simply rounded off into a knob, and no cirri are present. Such a knob might, indeed, be held as a sort of balancing organ, but when we consider the comparatively small size of the knob, and its lightness, compared with the size and weight of the column, this argument loses its force. It seems probable that the weight of the column alone was sufficient ballast for the crinoid, and that in the comparatively untroubled waters at the sea

bottom a position once assumed would be maintained unless altered by definite swimming movements of the crinoid. Slight adjustments of position might at any time be secured by motion of the arms, or of the cirri, where such were present.

It has been suggested by Carpenter that the comatulids seldom move about to any extent except during the breeding season. Clark (1909 *a*) confines the free-swimming period of multibrachiate comatulids to those stages in which a ten-armed condition obtains. During this stage the young, when observed, are continually swimming about. When the multibrachiate stage is assumed they are incapable of swimming movement. Whether or not this be the case it is hard to tell, but it seems likely that, in these forms at least, the adults are incapable of any considerable activity. This prohibition is obviously dependent upon the structure of the arms. This is of such a nature as to render any considerable motion impossible. It is conceivable, however, that the crinoids may crawl by employing the distal portions of their arms. In the case of adult detached crinoids as a whole there seems no physical disability in most cases rendering the crinoids incapable of using their arms as swimming organs. It seems probable, however, by the time an adult stage is reached that the crinoids will have found a favorable environment and under normal conditions would be content to remain there. Detachment from the bottom then need by no means indicate active swimming movements on the part of the animals involved. Indeed, among the stalked detached forms one may hold that the type of life led is essentially statozoic. As a rule advantage is taken of their freedom probably only during periods of sexual activity.

Eleutherozoic conditions as indicative of progression or degeneracy among the Pelmatozoa.—It should be borne in mind that the tendency toward an eleutherozoic existence among the crinoids is not a reversion, in the sense of indicating a loss of vigor in the stock, and degeneration. The freedom of the crinoid is rather an expression of a higher degree of specialization along perfectly natural lines. The discarding of the stem after a long period of attachment, as I see it, is a sign of strength rather than weakness, as indicating a tendency on the part of the organisms toward the elimination of semiuseless structures for the attainment of a type of life more beneficient to the crinoids. The fact that highly specialized eleutherozoic conditions do not more largely obtain among the Crinoidea is due in no small part to the fact, as has elsewhere been pointed out, that the animals in the main are not fitted for the efficient maintenance of this type of existence.

Among the Cystidea, on the other hand, the majority of the free forms may be considered degenerate. Indeed, lack of fixation among these types may be held as evidence of failure on their part to acquire the statozoic habit toward which they were aiming. Such a case is

that of *Pleurocystis*. Originally descended from a free form, a statozoic existence was acquired, which was maintained long enough to impress a degree of radial symmetry upon the theca, and for the acquisition of a jointed column. In the decadence of the stock a prostrate existence was gradually assumed, and the animals crawled about, dragging an all but useless stem behind them. Such a failure as regards the majority of the Cystidea well illustrates the fate of any major tendency becoming effective in a large body of organisms. When a group of animals tends to assume a decided change in structure and habit of life, the tendency becomes effective in varying degrees among different genetic lines. One or two lines, perhaps, out of the whole group will carry the innovation through successfully. The other members equally affected by the tendency, but incapable of pushing it to a successful issue, form short-lived lines that as a rule show obvious indications of degeneracy.

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EXPLANATION OF PLATES.

PLATE 1.

Aristocystis bohemicus Barrande.

Fig. 1. Specimen showing base of attachment and a side apparently smoothed and somewhat flattened by contact with some extraneous object. From Barrande, 1887. (Pl. 10, fig. 13.)

2. View of base, enlarged, showing attachment to a gastropod shell which is almost completely overgrown. From Barrande, 1887. (Pl. 10, fig. 16.)

3. Opposite side of the same specimen showing normal convexity and surface structure. From Barrande, 1887. (Pl. 10, fig. 13.)

4. Base of another individual showing no sign of attachment. From Barrande, 1887. (Pl. 10, fig. 20.)

5. Lateral view of a specimen which was completely detached. The smoothing of the plates in the upper right-hand portion of the figure indicates contact with some object, and may point to the maintenance of a prostrate existence. From Barrande, 1887. (Pl. 10, fig. 21.)

6. Basal view of the same specimen, showing rounded character of base and total absence of signs of attachment. From Barrande, 1887. (Pl. 10, fig. 22.)

7. Lower portion of theca of an individual which apparently was attached. The smoothing of the plates on one side is quite evident. From Barrande, 1887. (Pl. 10, fig. 29.)

8. The base of the same specimen, showing basal depression. It is to be noted that the area of attachment is somewhat excentric in position and that the smoothing of the plates may be attributed to contact with the object to which attachment was had. From Barrande, 1887. (Pl. 10, fig. 30.)

9. View of a very large, incomplete individual. The area of attachment is very large but not sharply defined. It is probable that in this case detachment was had late in the life of the organism. From Barrande, 1887. (Pl. 10, fig. 23.)

10. Basal view of the same, showing lateral position of the area of attachment. From Barrande, 1887. (Pl. 10, fig. 24.)

Echinosphæra aurantium (Gyllenhahl).

11. Lateral view of theca, showing highly excentric location of the minute protuberance that served as the point of attachment. From Jaekel, 1899. (Pl. 8, fig. 5.)

PLATE 2.

Cheirocrinus penniger Eichwald.

Fig. 1. View of antanal side with ramules restored. From Jaekel, 1899. (Pl. 11, fig. 1.)

2. View of anal side of the same specimen. The slight flattening of the theca and the great development of the anal area are especially to be noted. From Jaekel, 1899. (Pl. 11, fig. 2.)

Erinocystis volborthi Jaekel.

Fig. 3. Basal view of an individual, showing the marked flattening of one side and the carrying outward and backward of the anal opening. From Jaekel, 1899. (Pl. 13, fig. 6*a*.)

Pleurocystis filitextus Billings.

(See also Plate 3, fig. 3.)

4. Anal (lower) side, somewhat enlarged. Adapted from Jaekel, 1899. (Pl. 12, fig. 5.)

Arachnocystis infaustus (Barrande).

5. A specimen with the stem essentially complete. From Barrande, 1887. (Pl. 25, fig. 7.)
6. A portion of the column enlarged. From Barrande, 1887. (Pl. 25, fig. 8.)

Macrocystella mariæ Callaway.

7. Reconstruction of crown and stem by Bather. From Bather, 1900. (Text fig. 18, p. 56.)

Echinœncrinus angulosus (Pander).

8. Specimen showing flattening of the lower side of the theca, the posterior location of the anal opening, and the nature of the column. From Jaekel, 1899. (Pl. 13, fig. 18.)

Erinocystis angulata Jaekel.

9. Specimen showing the extreme outward and backward location of the anal opening. From Jaekel, 1899. (Pl. 13, fig. 16*a*.)

PLATE 3.

Placocystis forbesianus de Koninck.

Fig. 1. Convex upper (dorsal) surface of theca with a portion of the column. After Bather, 1900. (Text fig. 13, 1, p. 51.)
2. Flattened lower (ventral) surface showing adoral appendages ("spines"). After Bather, 1900. (Text fig. 13, 2, p. 51.)

Pleurocystis filitextus Billings.

(See also Plate 2, fig. 4.)

3. Specimen preserving a portion of the brachioles and an essentially complete column. Original in the collection of the University of Chicago.

Trochocystis bohemicus Barrande.

4. The terminal adoral hinged plate, approximately × 2. From Barrande, 1887. (Pl. 3, fig. 22.)
5. A complete column of this species, approximately × 2½. From Barrande, 1887. (Pl. 3, fig. 17.)

Mitrocystis mitra Barrande.

6. Lower (ventral) surface of theca with appended column. From Bather, 1900. (Text fig. 12, 1, p. 50.) After Barrande.
7. Convex upper (dorsal) surface. From Bather, 1900. (Text fig. 12, 2, p. 50.) After Barrande.
8. Inner surface of adoral portion of upper thecal wall, showing longitudinal corrugations on the central terminal plate. From Bather, 1900. (Text fig. 12, 3, p. 50.) After Barrande.

Anomalocystis disparilis Hall.

Fig. 9. Adoral (anterior) view of theca, showing terminal aperture and sockets for the articulation of the spines. Original in the United States National Museum, catalogue number 33661.

10. Lateral view of the same specimen.

11. Aboral view of the same individual showing deep, socket-like depression for the reception of the stem.

PLATE 4.

Isocrinus maclearanus Wyville Thomson.

Fig. 1. A complete individual, showing the extreme brevity of the column, approximately × 1. From Carpenter, 1884. (Pl. 16, fig. 1.)

Isocrinus decorus Wyville Thomson.

2. A very young specimen with a practically complete column, approximately × 2. From Carpenter, 1884. (Pl. 35, fig. 1.)

Woodocrinus macrodactylus de Koninck.

3. A complete individual, showing the tapering column with no evidence of structure for permanent fixation, approximately × 1. From Zittel, 1896. (Text fig. 265, p. 159.) After de Koninck.

PLATE 5.

Pentacrinus (*Extracrinus*) *collenoti* de Loriol.

Fig. 1. A portion of the cirrus, enlarged. After de Loriol, 1884–1889. (Pl. 198, fig. 1*b*.)

2. The distal ossicles of a cirrus, showing the terminal claw. After de Loriol, 1884–1889. (Pl. 198, fig. 1*h*.)

3. Articular face of a cirrus ossicle. After de Loriol, 1884–1889. (Pl. 196, fig. 1*d*.)

Cactocrinus proboscidialis (Hall).

4. Portion of three juxtaposed pinnules enlarged, showing close union effected by overlapping of the lateral processes on adjacent pinnules. After Wachsmuth and Springer, 1897. (Pl. 58, fig. 7*c*.)

5. A single pinnule ossicle greatly enlarged, showing the nature and relation of the lateral spinous process to the ossicle.

Lepadocrinus gebhardi (Conrad).

6. Portion of the column, showing discrete, articulated ossicles above, and the consolidated, terminal portion below. After Hall, 1859. (Pl. 7, fig. 5.)

7. Terminal fused portion of the column of another individual, showing a pustulose surface. After Hall, 1859. (Pl. 7, fig. 16.)

Brachiocrinus nodosarius Hall.

8. Distal portion of the column, showing its termination in a knob. Above may be noted the points of attachment for two of the lateral cirri. × 2. After Hall, 1859. (Pl. 6, fig. 2*a*.)

Ancyrocrinus bulbosus Hall.

9. Distal portion of the column showing the grapnel, the fused columnals, and above, some of the unaltered columnals. From Bather, 1900. (Text fig. 51, p. 134.) After Hall.

Actinometra paucicirra Bell.

Fig. 10, 11, 12. Specimens showing centro-dorsals from which all cirri have been lost. The variability in outline of the centro-dorsals is interesting, and shows how this character is governed by the contour of the surrounding and underlying plates. After Carpenter, 1888. (Pl. 54, figs. 3, 5, 7.)

Isocrinus wyville-thomsoni Jeffreys.

13. The terminal nodal of a detached individual showing how the columnal has been smoothed and rounded off by a secondary deposit of stereom; approximately ×4. From Carpenter, 1884. (Pl. 22, fig. 27.)

PLATE 6.

Millericrinus prattii (Gray).

Fig. 1. Individual showing practically resorbed stump of the column of which five columnals have been retained. After Carpenter, 1882. (Pl. 1, fig. 13.)
2. Specimen with a longer column, which shows signs of resorption in its distal portion. After Carpenter, 1882. (Pl. 1, fig. 10.)
3. Individual retaining but three columnals and showing no signs of resorption. After Carpenter, 1882. (Pl. 1, fig. 3.)
4. Basal view of another specimen the column of which is represented by the "proximale" and a single largely resorbed columnal. After Carpenter, 1882. (Pl. 1, fig. 2.)
5. View of the distal face of the "proximale," showing its insertion within the basal circlet. After Carpenter, 1882. (Pl. 1, fig. 22.)
6. The "proximale" and surrounding basals of an individual the column of which has otherwise entirely been lost. The resemblance of this "proximale" to a centrale is apparent. After Carpenter, 1882. (Pl. 1, fig. 6.)

Apiocrinus roissyanus d'Orbigny.

7. Specimen showing supernumerary plates comparable to those found in *Millericrinus prattii* as figured on this plate. After de Loriol, 1882–1884. (Pl. 43, fig. 3*a*.)

Apiocrinus elegans Defrance.

8. Specimen showing "intercalated" plates in the theca similar to those noted in *A. roissyanus*, fig. 7. After de Loriol, 1882–1884. (Pl. 34, fig. 4.)

Actinometra nobilis Carpenter.

9, 10, 11. Basal views of different specimens showing loss of cirri by the centro-dorsals, and the partial resorption of these organs. After Carpenter, 1888. (Pl. 65, figs. 3, 4, 5.)

PLATE 7.

Millericrinus charpyi de Loriol.

Fig. 1. A specimen showing the highly differentiated nature of the proximal columnal, to which three of the basals are still attached; approximately ×1½. After de Loriol, 1882–1884. (Pl. 100, fig. 1*c*.)

Millericrinus beaumonti d'Orbigny.

2. View of an individual showing the cup and proximal columnal. To the right and below is a view of the inferior face of the proximal columnal showing the petaloid type of articulation. After de Loriol, 1882–1884. (Pl. 90, figs. 3, 3*a*.)

Thiollericrinus heberti de Loriol.

Fig. 3. Lateral view of theca, showing great development of the proximal columnal and relative insignificance of the cup; approximately ×1½. After de Loriol, 1884–1889. (Pl. 228, fig. 2*a*.)

Thiollericrinus flexuosus Goldfuss.

4. View of theca and proximal columnal. In both this and the preceding figure it is to be noted that in the cup nothing but the radials appear externally. The appearance of irregularly placed cirri borne by the proximal columnal is likewise of interest; approximately ×1½. After de Loriol, 1884–1889. (Pl. 229, fig. 2*b*.)
5. Cup from below showing character of proximal columnal, and its type of articulation; ×2. After Bather, 1900. (Text fig. 117, 1, p. 195.)

Antedon phalangium (Müller).

6. Very early pentacrinoid stage, × 20. After Carpenter, 1888. (Pl. 14, fig. 1.)

Antedon tuberosa Carpenter.

7. Later pentacrinoid stage than that shown in figure 6; × 12. After Carpenter, 1888. (Pl. 14, fig. 9.)

Antedon multispina Carpenter.

8, 9, 10. Successive stages in the development of the centro-dorsal as shown by this species; all × 12. After Carpenter, 1888. (Pl. 14, figs. 5, 6, 7.)

Antedon sarsii Duben and Koren.

11, 12. Lateral view of some of the larval columnals of this species, and a view of the articular surface of one of the columnals; much enlarged. After Bather, 1900. (Text fig. 49, 8, 9, p. 132.) After Sars.

PLATE 8.

Antedon laticirra Carpenter.

Fig. 1, 2. Two views of the centro-dorsal of this species showing the irregular arrangement and relatively enormous size of the cirrus sockets; × 6. After Carpenter, 1880*a*. (Pl. 23, figs. 6*b*, 6*c*.)

Antedon (*Solanocrinus*) *scrobiculata* Goldfuss.

3. Side view of a specimen showing highly elongate centro-dorsal. After Carpenter, 1880*b*. (Pl. 10, fig. 14.) From Goldfuss.
4. Inferior aspect of dorsal cup showing petaloid type of articulation. After de Loriol, 1884–1889. (Pl. 214, fig. 3*c*.)

Pentacrinus (*Extracrinus*) *dargniesi* Terquem and Jourdy.

5. Basal view of a specimen from which the stem has been lost. For comparison with figures 4 and 7; approximately × 3. After de Loriol, 1884–1889. (Pl. 210, fig. 1*a*.)

Antedon incerta Carpenter.

6. A cirrus of this species to show the high degree of specialization acquired by these organs. Note the terminal claw and the spinous processes borne by the ossicles to perfect the appendages as grasping organs.

Antedon depressa d'Orbigny.

Fig. 7. Basal view of specimen from which the centro-dorsal has been removed; approximately × 2. After de Loriol, 1884–1889. (Pl. 221, fig. 1*a*.)

8. Lateral view of cup to which the centro-dorsal is attached; × 3. After De Loriol, 1884–1889. (Pl. 221, fig. 2*b*.)

PLATE 9.

Uintacrinus socialis Grinnell.

Fig. 1. Normal base of "Form D" with unusually large centrale. After Springer, 1901. (Pl. 2, fig. 10.)

2. Normal base of "Form D" with smaller centrale. After Springer, 1901. (Pl. 2, fig. 12.)

3. Base of "Form D" in which the centrale meets the basals as well as the infrabasals, and is decagonal in outline. The infrabasals are comparatively minute, but of equal size. After Springer, 1901. (Pl. 2, fig. 9.)

4. Base of "Form D" in which the centrale meets three of the basals. Two of the infrabasals are much smaller than the other three. After Springer, 1901. (Pl. 2, fig. 18.)

5. A varient of the foregoing in which the centrale has fused with one of the small infrabasals. After Springer, 1901. (Pl. 2, fig. 7.)

6. A base in which fusion has been carried still further. The centrale has here fused with two of the infrabasals. After Springer, 1901. (Pl. 2, fig. 6.)

7. A base in which in addition to the centrale becoming fused with two of the infrabasals, fusion has taken place between two of the other infrabasals. After Springer, 1901. (Pl. 2, fig. 5.)

8. Base in which fusion has taken place probably between the centrale and two of the infrabasals on the one hand, and between the three remaining infrabasals on the other. After Springer, 1901. (Pl. 2, fig. 4.)

9. A base of "Form M" in which fusion has been effected between two of the basals. After Springer, 1901. (Pl. 2, fig. 14.)

10. Base of "Form M" showing centrale of nearly minimum size. After Springer, 1901. (Pl. 2, fig. 2.)

11. Base of "Form M" showing centrale of maximum size. After Springer, 1901. (Pl. 2, fig. 1.)

Megistocrinus rugosus Lyon and Casseday.

12. View of fused basals, surrounded by the radials and proximal anal. It is to be noted that the fused basals form a regular pentagon with straight faces. After Wachsmuth and Springer, 1897. (Pl. 48, fig. 6*a*.)

PLATE 10.

Saccocoma tenella Goldfuss.

Fig. 1. Specimen showing cup and structure of arms. R=radial; c=centrale; ×7. From Bather, 1900. (Text fig. 68, 1, p. 155.) After Jaekel.

Saccocoma pectinata Goldfuss.

2. Complete individual to show coiling of the distal portions of the arms; ×½. From Bather, 1900. (Text fig. 68, 2, p. 155.)

3. Lateral view of cup and proximal arm ossicles; ×2½. R=radial. From Bather, 1900. (Text fig. 68, 3, p. 155.) After Zittel.

Marsupites testudinarius Schlotheim.

Fig. 4. Lateral view of cup. B=basal; c=centrale; IB=infrabasal; R=radial. From Bather, 1900. (Text fig. 104, 1, p. 185).

Agassizocrinus dactyliformis Troost.

5. Complete individual showing cup and arms. The infrabasals are here shown as not completely consolidated. From Meek and Worthen, 1873. (Pl. 21, fig. 7*a*.) After Roemer.

Eleutherocrinus cassedayi Shumard and Yandell.

6, 7, 8. Upper, lower, and adoral views of a fairly perfect specimen; ×2. From Whiteaves, 1889. (Pl. 14, figs. 5, 5*a*, 5*b*.)

PLATE 11.

Edriocrinus dispansus, new species.

Fig. 1. Lateral view.

2. View from above. Original in the collection of the United States National Museum, catalogue number, 27757.

Eudesicrinus mayalis (Deslongchamps) de Loriol.

3, 4, 5. Three greatly enlarged views of this species. The degree of magnification is shown by the small figure to the right and above fig. 3. After de Loriol, 1882–84. (Pl. 29, figs. 1, 1*a*, 1*b*, 1*c*.)

Cotylecrinus docens Deslongchamps.

6, 7, 8. Three views of this species, from below, the side, and above. Attachment is had in this case by growth of the base over a crinoid stem. After de Loriol, 1882–1884. (Pl. 20, figs. 1, 1*a*, 1*b*.)

Edriocrinus pyriformis Hall.

9. Side view, showing cup and elongate peduncle. After Hall, 1862. (Text fig. 1, p. 115.)

Holopus rangii d'Orbigny.

10. Complete individual, slightly enlarged. After Carpenter, 1884. (Pl. 2.)

Lichenoides priscus Barrande.

11. Basal view of a specimen showing entire absence of column attachment. After Barrande, 1887. (Pl. 1, fig. 21.)

Protocrinus oviformis Volborth.

12. Basal view of specimen showing point for attachment of the stem. It is to be noted that the proximal circlet consists of four plates. After Bather, 1900. (Text fig. 45, 2, p. 75.) After Volborth.

13. Basal view of another specimen which shows no signs of stem attachment; the basal circlet consists of but three plates, as a result of the fusion of two of the four plates shown in figure 12. After Bather, 1900. (Text fig. 45, 3, p. 75.) After Volborth.

Edriocrinus sacculus Hall.

14. A group of young attached individuals. Original in the collection of the United States National Museum, catalogue number, 57504.

15. Adult, free individual, crawling over the surface of a gastropod shell. Original in the collection of the United States National Museum, catalogue number, 57504.